Mechanistic underpinnings of foraging variability in the common sea star, *Asterias rubens*, from Newfoundland, Canada

by

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A thesis submitted to the
School of Graduate Studies
in partial fulfillment of the
requirements for the degree of
Master of Science

Department of Biology

Memorial University of Newfoundland

February, 2015

St. John's, Newfoundland, Canada

ABSTRACT

The common sea star, *Asterias rubens*, is a major predator in rocky subtidal ecosystems in the northern Gulf of St. Lawrence and along the Atlantic coast of Newfoundland. Yet, knowledge about the mechanistic underpinnings of foraging variability in *A. rubens* in these highly seasonal systems is sparse. The present research tested effects of key biotic (body size, starvation, chemical cues from potential competitors) and abiotic (temperature, wave action) factors on: 1) displacement, microhabitat selection, and ability to contact blue mussel, *Mytilus edulis*, prey; and 2) mussel prey consumption and size selection in *A. rubens* from southeastern Newfoundland. Experiments in laboratory microcosms (wave tank and aquaria), as well as analysis of seabed imagery and sea temperature and wave data from one subtidal site, showed that wave action, and to a lesser extent starvation, are key modulators of the sea star's inclination and ability to explore its environment and localize prey. In southeastern Newfoundland, the behavioral response of *A. rubens* to wave action and starvation is adaptable, being generally stronger in summer than winter, when sea temperature differs markedly. Starvation, body size, and their interaction strongly affect prey consumption and size selection. Consumption is relatively stable across the natural temperature range in late summer, significantly lower in winter than summer, and unaffected by the chemical presence of indigenous rock crab, *Cancer irroratus*, and invasive green crab, *Carcinus maenas*. Collectively, results speak to the importance of considering the interplay between organismal traits and ongoing changes in ocean climate to more accurately predict causes and consequences of alterations to northern reef communities.

ACKNOWLEDGEMENTS

I thank my supervisor Dr. Patrick Gagnon for continued encouragement and guidance throughout every stage of this project, as well as the other members of my supervisory committee, Dr. Suzanne Dufour and Dr. Iain McGaw for support and constructive comments that helped improve the thesis. Special thanks to the field team in the Gagnon lab for their hard work, constant help, and dedication; David Bélanger, Desta Frey, Caitlin Blain, and Kyle Millar, as well as to the laboratory research assistants Philippe Schryburt, Laura Purchase, Renee Roberts, Ítalo Lima, and Michelle Valliant. I thank Chantelle Penney for assistance with crab husbandry, Dr. David Schneider for statistical advice, and Ryan Stanley for help using R. I am also grateful for the support and encouragement of my family and friends. This research was funded by Natural Sciences and Engineering Research Council of Canada (NSERC Discovery Grant), Canada Foundation for Innovation (CFI Leaders Opportunity Funds), and Research & Development Corporation of Newfoundland and Labrador (IngniteR&D) grants to Patrick Gagnon. Anne Provencher St-Pierre was supported by the NSERC Canada Graduate Scholarship-Master's Program and the Fond de recherche du Québec - Nature et technologies (FRQNT) Masters research scholarship - B1 program.

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CO-AUTHORSHIP STATEMENT

The work described in the present thesis was conducted by Anne Provencher St-Pierre with guidance from Patrick Gagnon, Suzanne Dufour, and Iain McGaw. Anne Provencher St-Pierre was responsible for field and laboratory data collection and analysis (with assistance by Patrick Gagnon) and contributed to modifications brought to the original design by Patrick Gagnon. All chapters were written by Anne Provencher St-Pierre with intellectual and editorial input by Patrick Gagnon. Chapter II and Chapter III were submitted for publication in *Journal of Experimental Marine Biology and Ecology* and *Marine Biology*, respectively (full references below). Any additional publication in the primary literature resulting from work in the present thesis will be co-authored by Anne P. St-Pierre and Patrick Gagnon.

St-Pierre, A.P. & Gagnon, P. (submitted). Wave action and starvation modulate intra-annual variation in displacement, microhabitat selection, and ability to reach prey in the common sea star *Asterias rubens* Linneaus. *Journal of Experimental Marine Biology and Ecology*.

St-Pierre, A.P. & Gagnon, P. (revision requested). Mechanistic underpinnings of prey consumption and size selection in a major echinoderm predator. *Marine Biology.*

CHAPTER I

General introduction

Foraging is broadly defined as the sequence of activities of a consumer to acquire food (MacArthur and Pianka 1966; Begon et al. 1996; Fox et al. 2001). According to foraging theory, the basic sequence of activities yields a single prey (or food item) and is referred to as the "prey cycle". Four activity components make up the prey cycle: 1) search; 2) assessment; 3) pursuit and attack; and 4) handling of prey (Stephens and Krebs 1986; Fox et al. 2001). Consumers that forage on prey aggregated in discrete patches typically complete consecutive prey cycles in which the search is virtually eliminated because prey are in contact with, or very close to, one another. Successive prey cycles are therefore embedded within a broader "patch cycle" during which the consumer: 1) searches for a patch; 2) assesses its suitability; and 3) feeds upon it (Charnov 1976; Fox et al. 2001; Calcagno et al. 2014).

External and internal factors and processes affect the different components of the foraging process (Perry and Pianka 1997; Mills and Marchant-Forde 2010). The first component of the prey cycle, "search", involves prey detection through various combinations of tactile, visual, auditory, and chemical cues and signals (Stephens and Krebs 1986; Madsen et al. 2005; Catania et al. 2008; Hay 2009). Accordingly, mobile consumers typically attempt to increase rate of prey encounters by increasing displacement (Barbeau and Scheibling 1994b; Fox et al. 2001; Hill et al. 2002). However, the ability to displace varies with the morphology and physiology of the consumer and the environmental conditions to which it is exposed (Crist et al. 1992; Nathan et al. 2008). Because biological rate processes generally scale positively with increasing temperature, body size, and food intake, displacement (and most other physical tasks) of ectothermic

consumers is particularly affected by thermal environment, life stage, and prey abundance (Brockington and Clarke 2001; Gillooly et al. 2001; Brown et al. 2004b).

In the second component of the foraging process, "assessment", most consumers remotely assess the prey and decide whether to pursue the foraging sequence or to abandon the prey (Fox et al. 2001). Consumers tend to avoid prey that could damage their feeding apparatus (Juanes and Hartwick 1990; Smallegange and Van der Meer 2003; Hummel et al. 2011) or that would require a long handling time and high energy expenditure compared to the benefits derived from consumption (Hughes and Elner 1979; Barbeau and Scheibling 1994b; Norberg and Tedengren 1995; Matheson and Gagnon 2012b). Therefore, the history of interactions of a consumer with prey, size and morphology of the consumer and prey, as well as prey profitability (ratio of prey energy content to the time required for handling the prey) largely dictate the consumer's decision. Reduced prey abundance, which may cause food deprivation (starvation), may also influence this decision as consumers are generally less selective when food deprived (Emlen 1966; Werner and Hall 1974; Mills and Marchant-Forde 2010).

The last two components of the prey cycle, "pursuit and attack" and "handling", are affected by factors such as the ability of the prey to escape or resist the consumer, the presence of competitors, and the size and morphology of the consumer and prey (Boulding 1984; Salierno et al. 2003; Wong and Barbeau 2005). During a patch cycle, the assessment and exploitation of a patch of prey is based on the density, quality, and size of the patch, as well as on the presence of competitors, time spent travelling between previous patches, and abundance of patches in the habitat (MacArthur and Pianka 1966; Charnov 1976; Calcagno et al. 2014).

Shallow, subtidal reef ecosystems in seasonal seas exhibit considerable variation in water temperature and flows (Menge and Sutherland 1987; Siddon and Witman 2003; Schiel et al. 2004; Blain and Gagnon 2013). Foraging in ectothermic, mobile consumers in such systems is therefore particularly likely to be affected by intra-annual cycles of environmental variability (Sanford 2002; Rilov et al. 2005; Lauzon-Guay and Scheibling 2007; Frey and Gagnon (In press)). This effect may exacerbate in structurally complex habitats where seabed topography creates physical obstacles and unfavourable hydrodynamic conditions that hinder either components of the prey or patch cycles (Guichard and Bourget 1998; Guichard et al. 2001; Powers and Kittinger 2002; Atilla et al. 2005).

Sea stars of the genus *Asterias* are ectothermic, mobile consumers that form dense populations in many shallow seasonal reef ecosystems in the Northern Hemisphere (Franz et al. 1981; Clark and Downey 1992; Gaymer et al. 2001a; Byrne et al. 2013). The common sea star, *Asterias rubens*, is a dominant sea star in the northeastern Atlantic (Sloan 1980; Ellis and Rogers 2000; Byrne et al. 2013) and northwestern Atlantic (where it was previously referred to as *Asterias vulgaris*) (Himmelman and Dutil 1991; Clark and Downey 1992). In the western Atlantic, *A. rubens* occurs primarily in rocky subtidal habitats (Allen 1983; Himmelman and Dutil 1991; Gaymer et al. 2001a; Witman et al. 2003; Himmelman et al. 2005) from South Carolina to southern Labrador (Martinez and Martinez 2010). Across this geographic range the species is tolerant of relatively large fluctuations in sea temperature and salinity; 0-25°C and 14-36‰ (Smith 1940; Franz et al. 1981). *Asterias rubens* is a major predator in rocky subtidal ecosystems in the northern

Gulf of St. Lawrence and along the Atlantic coast of Newfoundland, Canada (Himmelman and Steele 1971; Himmelman and Dutil 1991; Gaymer et al. 2001a, b; Gaymer et al. 2004). In these highly seasonal systems, *A. rubens* primarily consumes bivalve prey, with a strong preference for the blue mussel, *Mytilus edulis* (Himmelman and Steele 1971; Gaymer et al. 2001a, b; Gaymer et al. 2004).

Knowledge about foraging in *A. rubens* in eastern Canada is largely based on a few laboratory and field studies in the northern Gulf of St. Lawrence, which examined prey preference, mussel (*M. edulis*) consumption and size selection, interspecific competition for prey, and displacement under various hydrodynamic conditions. Essentially, these studies showed that: 1) small [12-16 cm] *A. rubens* select small [<15 mm] mussels when the latter dominates [70%] dense mussel aggregates [beds and aquaria] but selects medium [15-30 mm] ones when mussels are half as abundant [Gaymer et al. 2001b]; 2) small [12-16 cm] *A. rubens* consistently select medium [15-30 mm] mussels whether a major competitor, the northern sea star, *Leptasterias polaris*, is present or not [Gaymer et al. 2002]; 3) small to large [8-24 cm] *A. rubens* select medium [15-30 mm] mussels in unusually deep mussel beds dominated [65%] by mussels >30 mm despite high densities of conspecifics and competitors [*L. polaris*] [Gaymer and Himmelman 2002]; 4) *A. rubens* exposed to unidirectional water flows displaces cross-current to better assess gradients of prey chemical cues and reorient displacement towards prey as required [Drolet and Himmelman 2004]; and 5) displacement of *A. rubens* towards *M. edulis* is more directed in the presence than absence of oscillatory water flows similar to those in natural habitats [Gagnon et al. 2003]. Collectively, these and several other related studies (Himmelman and Dutil 1991; Barbeau and Scheibling 1994a; Gaymer et al. 2004;

Himmelman et al. 2005; Gaymer and Himmelman 2013) established that *A. rubens* is a highly selective predator, even when prey abundance is limiting. But they also suggest that foraging in *A. rubens* is governed by a complex suite of biotic and abiotic factors. More studies are required to separate the individual effects of each factor and measure the strength of their interactions.

This thesis aims to test effects of key biotic (body size, starvation, chemical cues from potential competitors) and abiotic (temperature, wave action) factors on: 1) displacement, microhabitat selection, and ability to contact mussel [*M. edulis*] prey; and 2) mussel prey consumption and size selection in *A. rubens* to gain a better understanding of the mechanistic underpinnings of foraging variability for the species. Work involves experiments in laboratory microcosms (wave tank and aquaria) at the Ocean Sciences Center of Memorial University of Newfoundland with *A. rubens* from various subtidal sites along the south shore of Conception Bay, as well as analysis of seabed imagery and temperature and wave data from Bread and Cheese Cove (BCC) in Bay Bulls, southeastern Newfoundland.

Chapter II tests the hypothesis that wave action and starvation modulate displacement, microhabitat selection, and ability of *A. rubens* to contact mussel (*M. edulis*) prey. Specifically, it uses an oscillatory wave tank that mimics the back-and-forth flow caused by waves in shallow subtidal habitats to quantify, at three wave velocities: 1) linear displacement, dislodgement, and time spent in six microhabitats mimicking natural seabed heterogeneity [Experiment 1]; and 2) ability to contact mussels [Experiment 2], in small, fed and moderately starved sea stars. Both experiments are carried out in two seasons when sea temperature differs markedly to quantify intra-annual

variation in the effects of wave action and starvation. It also 3) studies relationships between changes over six months in the abundance of *A. rubens* and the wave and temperature environment at three depths at BCC.

Chapter III tests the effects of water temperature, starvation, body size, and chemical cues from potential crustacean competitors on mussel (*M. edulis*) consumption and size selection in *A. rubens*. Specifically, it quantifies 1) consumption of medium mussels by small sea stars fed or starved moderately at three temperatures representative of middle-to-late summer highs and one temperature typifying late winter lows [Experiment 1]; 2) consumption of small, medium, and large mussels by small and large sea stars fed or starved moderately or severely [Experiment 2]; and 3) consumption of small, medium, and large mussels by small sea stars starved moderately, in the presence or absence of chemical cues from *C. irroratus*, *C. maenas,* and crushed mussels [Experiment 3].

Chapter II and III are written in a format compatible with the publication of scientific articles, which explains the repetition of core information, as well as the use of first-person plural pronoun ("we") and possessive determiner ("our"). Chapter IV summarizes the main findings and their contribution to advancing knowledge about the limits of tolerance, behavioral adaptability, and feeding plasticity of *A. rubens* to environmental variability. It also discusses directions for future research in this area.

CHAPTER II

Wave action and starvation modulate intra-annual variation in displacement, microhabitat selection, and ability to contact prey in the common sea star, *Asterias rubens*

2.1 INTRODUCTION

Organisms in high-latitude, shallow reef ecosystems are generally exposed to considerable intra-annual variation in hydrodynamic and thermal regimes (Menge and Sutherland 1987; Siddon and Witman 2003; Schiel et al. 2004; Blain and Gagnon 2013). There is mounting evidence from studies in temperate and subarctic seas that displacement towards, and consumption of prey by mobile, benthic consumers, are largely controlled by wave action, water temperature, and their interaction (Sanford 2002; Rilov et al. 2005; Matheson and Gagnon 2012b; Frey and Gagnon (In press)). Understanding how both factors affect displacement, habitat use, and access to prey in functionally important consumers is essential to more accurately predict changes in reef community dynamics, especially in the face of a changing ocean climate (Halpern et al. 2008; Burrows et al. 2011; Kordas et al. 2011; Harley 2013; Frey and Gagnon (In press)).

The common sea star, *Asterias rubens* (formerly *Asterias vulgaris*, Clark and Downey 1992), is a major predator in the rocky subtidal zone in the northern Gulf of St. Lawrence and along the Atlantic coast of Newfoundland, Canada (Himmelman and Steele 1971; Himmelman and Dutil 1991; Gaymer et al. 2001a, b; Gaymer et al. 2004). Knowledge about the ecology of *A. rubens* in these highly seasonal systems is largely limited to observational data and laboratory and field experiments that investigated competitive interactions for prey with the northern sea star, *Leptasterias polaris* (Morissette and Himmelman 2000b, a; Gaymer et al. 2001a, b; Gaymer et al. 2004). None of these studies specifically examined how wave and thermal environments may affect displacement, habitat use, and prey access in *A. rubens*. To our knowledge, the only study that explored effects of the wave environment on displacement in *A. rubens* is that by

Gagnon et al. (2003). According to the latter study, displacement of *A. rubens* in the presence of blue mussels, *Mytilus edulis*, the sea star's preferred prey in eastern Canada (Gaymer et al. 2001b; Gaymer et al. 2004; Scheibling and Lauzon-Guay 2007), can be up to two times higher in the absence than in the presence of waves, and more directed towards mussels in the presence than absence of waves (Gagnon et al. 2003). Although useful, this kind of information does not allow the identification of threshold wave velocities above which the sea star may exhibit shifts in habitat use to reduce, for example, the risk of being dislodged as seen in the green sea urchin, *Strongylocentrotus droebacheinsis* (Frey and Gagnon (In press)). It is also of limited value in estimating patterns of displacement in natural habitats, where prey distribution is typically patchy and abundance varies in space and time (Himmelman 1984, 1991; Gaymer et al. 2001a; Witman and Dayton 2001).

In general, predators have intermittent access to prey resources because of spatial and temporal variation in prey distribution and abundance (Begon et al. 1996; Krebs 2001; Witman and Dayton 2001). Many echinoderms attempt to increase displacement and feeding in response to the physiological stress caused by starvation (deprivation of nourishment) (McClintock and Lawrence 1985; Hart and Chia 1990; Brusca and Brusca 2003). A number of studies have used various starvation times to standardize hunger levels among *A. rubens* or other species of sea stars prior to experimentation (e.g. Sloan 1980; Barbeau and Scheibling 1994b; Gaymer et al. 2001b, 2002; Wong and Barbeau 2005). However, no study has specifically examined how starvation and its likely interaction with wave and thermal environments may affect the ability of *A. rubens* to displace, choose certain habitats over others, and access prey.

In the present study, we use two experiments in laboratory microcosms and field observations to test the hypothesis that wave action and starvation modulate displacement, microhabitat selection, and ability to contact prey in *A. rubens*. Specifically, we use an oscillatory wave tank that mimics the back-and-forth flow caused by waves in shallow subtidal habitats to quantify, at three wave velocities: 1) linear displacement, dislodgement, and time spent in six microhabitats [Experiment 1], and 2) ability to contact mussel prey [Experiment 2], in fed and starved, adult-sized *A. rubens*. We carry out both experiments in two seasons when sea temperature differs markedly (~2°C and 13°C) to quantify intra-annual variation in the effects of wave action and starvation. We also 3) study relationships between changes over six months in the abundance of *A. rubens* and the wave and temperature environment at three depths at one subtidal site in southeastern Newfoundland.

2.2 MATERIALS AND METHODS

2.2.1 Collection and acclimation of organisms prior to experimentation

The two experiments in this study, Experiment 1 and Experiment 2 (see sections 2.2.2 and 2.2.3), were conducted with *Asterias rubens* hand collected by divers in January, February, and August, 2013. Sea stars were collected at depths of 6 to 15 m from gently sloping bedrock platforms between Kings Cove (47°36'15.07" N, 52°52'55.17" W) and Lower Horse Cove (47°34'27.38" N, 52°54'13.38" W) in Conception Bay, Newfoundland (Canada). Sea stars were transported in large containers filled with seawater to the Ocean Sciences Centre (OSC) of Memorial University of Newfoundland.

Upon arrival at the OSC (<6 hours after collection), the sea stars were transferred to 330-L holding tanks supplied with ambient flow-through seawater pumped in from a depth of ~5 m in the adjacent embayment, Logy Bay, and sorted by size. We kept all 5-armed individuals with a body diameter of 9 to 15 cm (length of the longest axis between two opposing arm tips, measured with a vinyl tape with a precision of 0.5 mm) that clung or displaced readily in the tank, indicating the podia functioned normally. We chose this size class because 1) individuals of this size are sexually mature (Nichols and Barker 1984; Himmelman and Dutil 1991), therefore eliminating variation in foraging from potential behavioral differences between mature and non-mature individuals, and 2) it was the most abundant size class at times of collection.

Sea stars used in both experiments were then divided into two acclimation groups prior to experimentation: "fed" and "starved". Fed sea stars were offered live blue mussels, *Mytilus edulis*, during the three weeks preceding trials. Starved sea stars were unfed during those three weeks. Both experiments were conducted over several weeks, which required that we create and maintain multiple groups of sea stars at various stages of starvation within the 330-L holding tanks. This was done by isolating sea stars of a same acclimation group and designated week of usage in 10-L plastic containers, with eight to 10 individuals per container. Each container was covered with nylon netting of 1 mm mesh to prevent escape and allow water circulation. Every three or four days, we removed empty mussel shells from each container and added 100 to 150 mussels of 10 to 45 mm in shell length, providing sea stars with continual access to mussel tissues. We used a starvation of three weeks to mirror intermediate starvation times in other studies of sea stars in eastern Canada, including *A. rubens* (Barbeau and Scheibling

1994b; Rochette et al. 1994; Gaymer et al. 2001b, 2002; Wong and Barbeau 2005). In *A. rubens*, a 3-week starvation is long enough to initiate the release of reserve material from the pyloric caeca, but not so long as to provoke a general autolysis and body shrinkage that occurs during longer starvation times (Hancock 1958; Jangoux and van Impe 1977). Mussels offered to the sea stars during the acclimation and experiments were hand collected by divers at Foxtrap (47°30'47.51" N, 52°59'50.71" W) and Petty Harbour (47°27'50.78" N, 52°42'25.47" W). They were transported in large containers filled with seawater to the OSC within six hours after collection, and kept in 330-L holding tanks supplied with ambient flow-through seawater.

2.2.2. Displacement and microhabitat selection (Experiment 1)

To investigate intra-annual variation in the effects of wave action and starvation on displacement and microhabitat selection by *Asterias rubens*, we conducted a microcosm experiment, Experiment 1, in an oscillatory wave tank. The tank mimicked the back-and-forth flow caused by waves in shallow subtidal habitats (Figure 2.1, Gagnon et al. 2003). The experiment was conducted in February and March (hereafter termed winter) 2013, and again in September and October (summer) 2013, to test the predictions that the displacement of sea stars, and frequency of association with topographically uneven microhabitats, are respectively lower and higher 1) in winter than summer, 2) at high than low wave velocities, and 3) in starved than fed individuals. These predictions stem from the arguments that in the colder waters of winter, sea stars should be less active

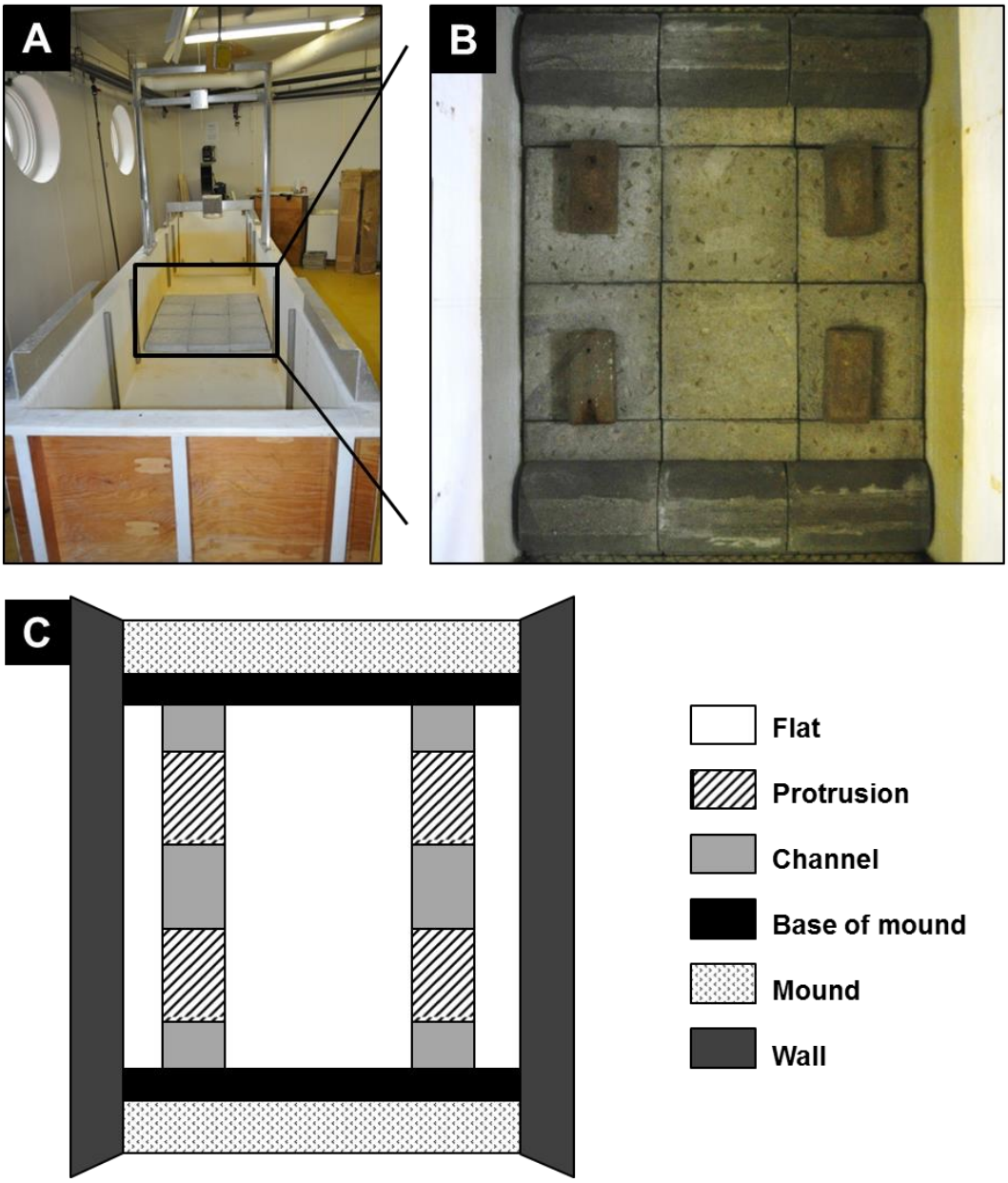

Figure 2.1. (A) Oscillatory wave tank and location of the experimental area [3 x 4 grid of concrete tiles of 0.3 x 0.3 x 0.05 m each], and (B) relative position of the four rectangular and six semi-circular concrete blocks used to create the protrusion, base of mound, and mound microhabitats in Experiment 1. (C) Location of the six microhabitats within the experimental area (see Section 2.2.2 for details).

and more inclined to cling to uneven surfaces that provide a good purchase to avoid dislodgement (1st prediction), as observed in winter at many subtidal sites in eastern Canada (P. Gagnon, personal observations). The latter effect should exacerbate with increasing wave action, for greater hydrodynamic forces generally reduce displacement in benthic organisms (2nd prediction) (Denny 1988; Kawamata 1998; Siddon and Witman 2003; Frey and Gagnon (In press)). Starved sea stars should also displace less and cling to uneven surfaces more frequently than fed individuals because of decreasing reserve material in starved individuals (3rd prediction) (see Section 2.2.1).

Two sea stars fed or starved three weeks (see Section 2.2.1) were allowed to displace and make contact with six microhabitats (see below) at three wave velocities: 0.0 m s^{-1} (Null), 0.1 m s^{-1} (Low), and 0.2 m s^{-1} (High) (peak longitudinal velocity measured with a Doppler current meter [Vector Current Meter; Nortek] at ~5 cm above the centre of the experimental area without the structures used to create the microhabitats). We used two sea stars in each trial to account for possible interactions during displacement and to represent the typical *A. rubens* density in eastern Canada, ~1-2 individuals m^{-2} (Himmelman and Dutil 1991; Gaymer et al. 2001a; Gaymer and Himmelman 2002). Wave velocity included the threshold value of ~0.2 m s^{-1} above which the displacement and ability of most sea stars to attach to the substratum in the tank were greatly reduced as determined from preliminary trials. We used a fixed frequency of 15 wave cycles min^{-1} in treatments with waves because 1) we were interested in the effects of water velocity on displacement and microhabitat selection, rather than the

effects of wave frequency per se, and 2) it reflects the general wave frequency under moderate winds at our collection and survey sites (see Section 2.2.4).

Trials were conducted on a 3 x 4 grid arrangement of concrete tiles (12 tiles, 0.3 x 0.3 x 0.05 m [L, W, H] each) (Figure 2.1). The grid was located in the center of the tank. It was delimited longitudinally by the tank walls and transversally by nylon netting of 2.5-cm mesh to restrict the sea stars to the experimental area. Preliminary trials showed no effect of netting on flow direction and speed. The upper surface of the tiles was sculpted with holes and cracks to simulate natural bedrock heterogeneity and rugosity. Sea stars had access to six microhabitats: 1) flat; 2) protrusion; 3) channel; 4) base of mound; 5) mound; and 6) wall. The surface area of these microhabitats was respectively 0.480, 0.224, 0.078, 0.083, 0.280, and 0.350 m^2, yielding an experimental area of 1.495 m^2 (Figure 2.1). The free surface of the tiles making up the bottom of the experimental area formed the flat microhabitat. Two pairs of rectangular concrete blocks (0.2 x 0.1 x 0.06 m each) located at 10 and 15 cm from the longitudinal tank walls and transverse mounds (see below) formed the protrusion microhabitat. These blocks together with mounds delimited open spaces, which formed the channel microhabitat. The base and upper portion of semi-circular concrete blocks (0.3 x 0.2 x 0.1 m each), which edged the base of the two transverse nettings, formed the base of mound, and mound microhabitats, respectively. The longitudinal tank walls flanking the experimental area formed the wall microhabitat. Sea stars in these microhabitats provided an indication of their inclination and ability to: 1) remain on horizontal surfaces like in barrens and underneath seaweed canopies [flat]; 2) associate with steeply sloping, low-profile points such as small and abrupt rocks and rocky outcrops [protrusion]; 3) move to tight spaces

such as crevices and in between adjacent rocks [channel]; 4) associate with the base of gently sloping, low-profile points such as the base of small rounded boulders [base of mound]; 5) move on top of gently sloping, low-profile points such as the top of small rounded boulders [mound]; and 6) move to and associate with steeply sloping, vertical surfaces like large rocky cliffs [wall]. Water velocity differed among microhabitats, ranging from 0.061 m s^{-1} (channel) to 0.234 m s^{-1} (mound), and from 0.105 m s^{-1} (channel) to 0.277 m s^{-1} (mound) for the low and high wave velocity treatments, respectively (Table 2.1). While in using this approach effects of microhabitats are confounded by those of water velocity, it is an accurate representation of the conditions to which sea stars are exposed in natural habitats. We were interested in the combined effect of both factors as opposed to their individual effects.

Each trial lasted 30 minutes to allow sufficient time for sea stars to contact at least one "non-flat" microhabitat at all wave velocities as determined from preliminary trials. Two sea stars were introduced, oral surface down, to the center of the experimental area, at a distance of 20 to 25 cm from each other. Sea stars were held in place by gently pushing the centre of the oral disc downward with a stick for one minute prior to the start of the trial. This procedure, which stimulated the attachment of podia to the concrete tiles, was necessary to allow sea stars in the two treatments with waves to adapt to the changing hydrodynamic forces and avoid dislodgement. In trials with waves, the motor was turned on after the first 30 seconds of this 1-min acclimation time. Sea stars were allowed to move freely in the experimental area for the following 30 minutes. The experimental area was photographed at 1-min intervals with a digital camera (D5000; Nikon) located 1.3 m above the water surface.

Table 2.1. Mean (±SE) peak longitudinal water velocity (m s^{-1}) in each of the six microhabitats in Experiment 1 and top of mounds and center of the depression in Experiment 2 for the low (0.1 m s^{-1}) and high (0.2 m s^{-1}) wave velocity treatments (see Sections 2.2.2 and 2.2.3 for a description of each experiment).

		Wave velocity treatment	
		Low	**High**
Experiment 1	Flat	0.096 (0.002)	0.147 (0.001)
	Protrusion	0.090 (0.001)	0.155 (0.001)
	Channel	0.061 (0.001)	0.105 (0.001)
	Base of mound	0.100 (0.002)	0.179 (0.001)
	Mound	0.158 (0.004)	0.277 (0.003)
	Wall	0.098 (0.001)	0.148 (0.001)
Experiment 2	Top of mounds	0.118 (0.001)	0.252 (0.002)
	Bottom of depression	0.074 (0.001)	0.149 (0.002)

We used the images of the experimental area, PhotoImpact X3 (Ulead Systems Inc.), and Image J (National Institutes of Health) to determine for each sea star in each trial: 1) the total displacement, defined by the sum of the linear distances moved from one image to the next, and 2) the proportion of time during which the sea star was dislodged, estimated by the ratio of the number of images in which the sea star had flipped on the aboral side, or had detached from the bottom and was being rocked by waves, to the total number of images used for the trial. We also determined 3) the proportion of time spent in each microhabitat, as estimated by the ratio of the number of images in which the sea star was in contact with each microhabitat to the total number of images used for the trial. Images in which the sea star had detached from the bottom were not included in calculations of displacement and proportion of time in each microhabitat. The proportion of time in each microhabitat was corrected for differences in surface area among microhabitats. This was done by multiplying the proportion of time in the microhabitat by the ratio of the surface of the microhabitat to the surface of the entire experimental area (1.495 m^2), for example 32% for the flat microhabitat. The corrected proportion of time was then divided by the sum of corrected proportions of time spent in all of the six microhabitats, yielding the standardized proportion of time spent in the microhabitat. Complementary trials carried out under a paired comparison design indicated that the distance moved by one sea star was not affected by the presence of the other sea star (see Appendix A). Statistical analyses were therefore run on the average displacement and proportion of time spent in each microhabitat from both sea stars (see Section 2.2.6).

Each of the six combinations of wave velocity and starvation treatments was replicated 11 times in winter (28 February to 30 March) and summer (3 September to 2

October), 2013. We blocked trials over time within each season by running one replicate of each treatment within a same day. The order of the treatments was randomized within each day. Concrete tiles in the grid and blocks forming the mounds were reshuffled randomly between trials. Each trial was run with sea stars not used previously. The relatively long (~2 h) flushing time of the wave tank prevented running each trial with new seawater. On each day the tank was filled with new seawater, which was used to conduct the first three trials, emptied, and filled again with new seawater to conduct the last three trials. Water temperature in the wave tank was recorded in each trial with a temperature logger with a precision of ±0.5°C (HOBO Pendant; Onset Computer Corporation). It averaged 1.9°C (±0.1) and 13.2 °C (±0.1) in the winter and summer trials, respectively.

2.2.3. Ability to contact prey across gradients of wave action (Experiment 2)

To investigate intra-annual variation in the effects of wave action and starvation on the ability of *Asterias rubens* to contact prey, we conducted a microcosm experiment, Experiment 2, in the oscillatory wave tank described in Experiment 1. The experiment was conducted in February and March (winter) 2013, and again in September (summer) 2013, to test the predictions that the ability to contact prey is lower: 1) in winter than summer, 2) at high than low wave velocities, and 3) in fed than starved individuals. These predictions stem from the same arguments as in Experiment 1. One sea star fed or starved three weeks (see Section 2.2.1) was allowed to displace on the flat bottom of a depression and climb on its convex sides and flattened top where prey, when present, were located

(see below and Figure 2.2), at wave velocities of: 0.0 m s^{-1} (Null), 0.1 m s^{-1} (Low), and 0.2 m s^{-1} (High). We used these wave velocities and a frequency of 15 wave cycles min^{-1} in treatments with waves for reasons given in Experiment 1. We used one sea star in each trial because we were interested in the individual ability of *A. rubens* to contact prey.

Trials were conducted on a 3 x 3 grid arrangement of the same tiles used in Experiment 1, also located in the centre of the tank (Figure 2.2). The tile in the middle of the grid formed the bottom of a square, 0.09-m^2 depression, which sides were made up of semi-circular concrete blocks (0.3 x 0.2 x 0.1 m each), hereafter termed "mounds". The grid contour was delimited longitudinally by the tank walls and transversally by nylon netting of 2.5-cm mesh to restrict the sea star to the experimental area. Preliminary trials showed no effect of netting on flow direction and speed. This arrangement yielded a gradient of wave velocities in treatments with waves, from lowest on the bottom of the depression to highest on the top of mounds (Table 2.1). In treatments with prey (50% of the trials), one nylon mesh bag (1 mm mesh size) containing 75 to 100 live blue mussels, *Mytilus edulis*, of 10 to 55 mm in shell length, was secured with small weights to the top of each mound, i.e. in the zone of maximum wave velocity (Table 2.1, Figure 2.2). We placed prey on top of the mounds to force *A. rubens* to move across gradients of wave velocity, like it does in natural habitats in search of sessile prey located in shallower areas or on topographically higher points. The loose arrangement of mussels in the bags allowed them to open their valves, while not being pushed away by waves. One empty nylon mesh bag was secured with weights to the top of each mound in treatments with no prey (50% of the trials, used as a control to separate effects of wave action and the presence of prey).

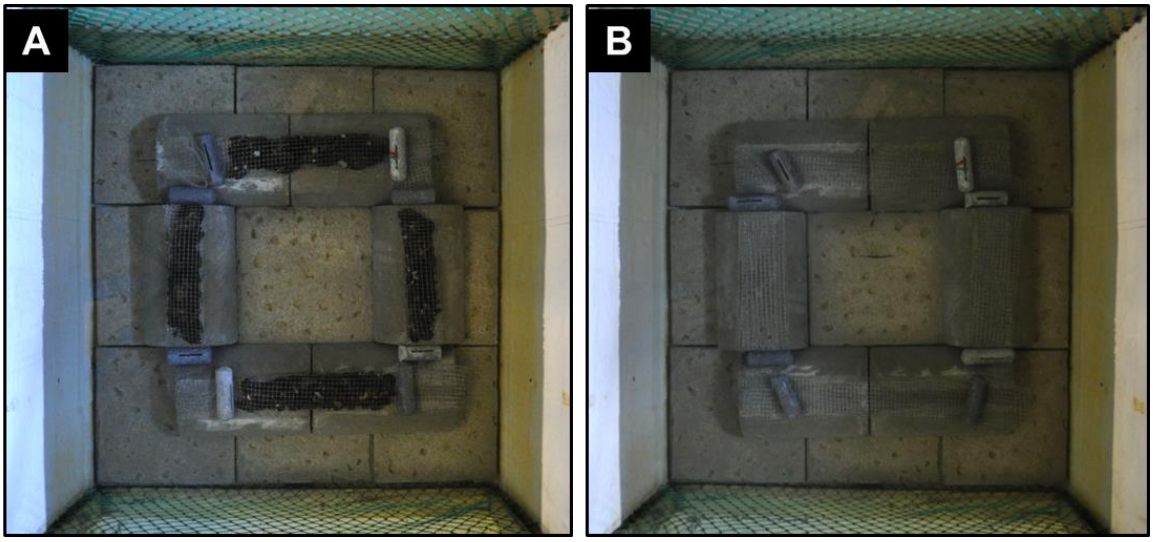

Figure 2.2. Experimental area [3 x 3 grid of concrete tiles of 0.3 x 0.3 x 0.05 m each] and position of the semi-circular concrete blocks used to create mounds and the central depression (0.3 x 0.3 m) to which one sea star (*Asterias ruben*) was introduced at the onset of trials (A) with, and (B) without mussels (*Mytilus edulis*) in Experiment 2 (see Section 2.2.3 for details).

Each trial lasted 30 minutes allowing sufficient time for sea stars to reach the top of at least one mound at all wave velocities as determined from preliminary trials. One sea star was introduced, oral surface down, to the centre of the depression and allowed to attach podia to the concrete tile for one minute. In trials with waves, the motor was turned on after the first 30 seconds of this 1-min acclimation time. Sea stars were allowed to move freely in the experimental area for the following 30 minutes. The experimental area was photographed every minute with a digital camera (D5000; Nikon) located 1.3 m above the water surface. We used the images of the experimental area, PhotoImpact X3 (Ulead Systems Inc.) and Image J (National Institutes of Health) to determine for each trial: 1) whether the sea star reached the top of at least one of the mounds, and 2) the proportion of time, if any, that the sea star spent on top of the mounds. The latter variable was approximated by the ratio of the number of images in which the sea star was in contact with the top of any of the mounds to the total number of images used for the trial. For both variables we discarded images in which the sea star had flipped on the aboral side or had detached and was being rocked by waves.

Each of the 12 combinations of wave velocity, starvation, and prey treatments was replicated 11 times in winter (25 February to 29 March) and summer (2 September to 29 September), 2013. Experiments 1 and 2 were therefore conducted concurrently to avoid confounded time effects, which enabled comparing results between experiments. We blocked trials over time within each season by running one replicate of each treatment within a same day. The relatively long (~2 h) flushing time of the wave tank prevented running each trial with new seawater. On each day the tank was filled with new seawater,

which was used to conduct the first six trials, emptied, and filled again with new seawater to conduct the last six trials. Because of this and to avoid exposing sea stars in treatments with no prey to waterborne chemicals from prey, we ran the six trials of a same prey treatment consecutively, followed by the six trials of the other prey treatment, with one water change in between the two groups of trials. The order of prey treatments, as well as that of wave velocity and starvation treatments within each prey treatment, was determined randomly for each day. Concrete tiles in the grid and the blocks that formed the mounds were reshuffled randomly between trials. Each trial was carried out with sea stars not used previously. Water temperature in the tank was recorded in each trial with a temperature logger (see Section 2.2.2). It averaged 2.1°C (±0.1) and 13.4°C (±0.1) in the winter and summer trials, respectively.

2.2.4. Distribution and abundance of *A. rubens*

To evaluate the variability in the distribution and abundance of *Asterias rubens* and its relationship to the temperature and wave environments, we studied changes over seven months in: 1) the density of *A. rubens* at multiple depths at Bread and Cheese Cove [BCC, 47°18'30.78" N, 52°47'19.12" W] on the north shore of Bay Bulls [Newfoundland], and 2) temperature and wave conditions in BCC. The seabed at BCC is composed of gently sloping bedrock to a depth of ~15 m, with scattered boulders between 3 and 5 m. Patchy kelp beds (mainly *Alaria esculenta* and *Laminaria digitata*) dominate the 0-2 m depth range, followed by an extensive urchin (*Strongylocentrotus*

droebachiensis) barrens with transient *Desmarestia viridis* beds to a depth of ~15 m (Blain and Gagnon 2014).

Sea star density was estimated from videos of the seabed at BCC acquired in 2011 as part of a research examining variability in the distribution and abundance of benthic seaweeds and macrofauna. A comprehensive description of the sampling protocol is provided in Blain and Gagnon (2014). Essentially, divers filmed a 1-m swath of seabed on each side of one permanently marked, 20- to 25-m benchmark line running parallel to the shoreline at 2, 4, and 8 m depths biweekly from 8 March to 13 October, 2011. These depths encompass the typical vertical range of *A. rubens* based on previous observations. Shallow (<4 m) depths were more intensively sampled because this is where the abundance of large invertebrate consumers, including *A. rubens*, is more likely to vary in response to generally more variable temperature and wave conditions than in deeper (8 m) water (Blain and Gagnon 2013; Gagnon et al. 2013; Blain and Gagnon 2014). This procedure yielded two video transects per depth on each sampling date. Each video transect was converted into one image strip and segmented into 12 to 25 frames (depending on clarity) of 0.8 m^2. In the current study, we counted and divided the number of sea stars >5 cm in diameter (the smallest detectable size on the imagery) in each of five haphazardly selected frames without fleshy seaweeds, by the surface area of the frame, yielding 10 density estimates per depth on each sampling date. Sea stars underneath seaweed canopies, if any, were not visible from the imagery and hence could not be accounted for. Accordingly, we used only those frames with no seaweed canopy, i.e. with a 100% open surface, to eliminate possible bias. We analyzed frames from videos

acquired on 25 April, 2011 and every 20 to 40 days until 13 October 2011, yielding seven, approximately monthly samples.

The sea temperature at BCC was recorded every 60 min throughout the survey with a temperature logger (±0.5°C, HOBO Pendant; Onset Computer Corporation) attached to one eyebolt drilled into the seabed at 3 and 9 m depths. The wave environment was quantified by recording the pressure of the water column on the seabed was recorded every minute by a water level logger secured to the seabed with eyebolts at a depth of 12 m (Blain and Gagnon 2013; Frey and Gagnon (In press)). Raw pressure values (psi) were corrected for barometric pressure by subtracting the hourly atmospheric pressure (psi) at the date and time of measurement (http://www.climate.weather.gc.ca/, Station St. John's Intl A). Each corrected value was then converted into a raw water depth (m) by multiplying it by a conversion factor of 0.68 m psi^{-1} (NOAA 2001). Raw water depths were corrected for tidal elevation and logger depth by subtracting the elevation at the date and time of measurement (http://www.tides.gc.ca/eng, Station 905) and the exact depth of the logger, yielding wave height.

2.2.5 Statistical analysis

Experiment 1: We used two three-way ANOVAs with the factors Season (winter and summer trials), Wave (null, low, and high wave velocity), and Starvation (fed and starved sea stars), to examine intra-annual variation in the effects of wave action and starvation on 1) the mean displacement of sea stars and 2) the proportion of time during which sea stars were dislodged. Prior to running these three-way ANOVAs, we used one-way ANOVAs for each season with the factor Block (each daily block of one replicate of each

treatment) to determine if results differed among blocks in each season. There was no significant effect of the factor Block for displacement ($F_{10,55}$=0.46, p=0.91 in winter, and $F_{10,55}$=0.87, p=0.56 in summer) and proportion of time dislodged ($F_{10,55}$=0.80, p=0.63 in winter, and $F_{10,55}$=0.62, p=0.79 in summer). We therefore ran the two three-way ANOVAs on data pooled from all blocks. We treated the analysis of the proportion of time dislodged as a particular case of the generalized linear model to correct for heteroscedasticity and deviation of residuals from normality detected in the first place with a classical linear model. We used a binomial distribution of the residuals because the response variable was a proportion (McCullagh and Nelder 1989; Bolker et al. 2008). No binomial variation was detected. The three-way ANOVAs were applied to the raw data (n=132).

We used a three-way permutational MANOVA (Euclidean distance matrices with 999 permutations) with the factors Season (winter and summer trials), Wave (null, low, and high wave velocity) and Starvation (fed and starved sea stars), to examine intra-annual variation in the effects of wave action and starvation on the mean proportion of time spent by sea stars in each of the six microhabitats (Flat, Protrusion, Channel, Base of mound, Mound, and Wall). Prior to running this MANOVA, we used a one-way permutational MANOVA for each season (n=66) with the factor Block (each daily block of one replicate of each treatment) to determine if results differed among blocks in each season. There was no significant effect of the factor Block in winter ($F_{10,55}$=0.91, p=0.55) and summer ($F_{10,55}$=0.69, p=0.82). Accordingly, we ran the three-way MANOVA on data pooled from all blocks. The three-way MANOVA was applied to the raw data (n=132). When a factor or interaction between factors was significant in the MANOVAs, we

examined the univariate model for the response variables to identify which one(s) contributed to the multivariate effect. This was done by conducting an ANOVA for the response variable with those factors that were significant in the MANOVA (Scheiner and Gurevitch 2001).

Experiment 2: We used a four-way ANOVA with the factors Season (winter and summer trials), Wave (null, low, and high wave velocity), Starvation (fed and starved sea stars), and Prey (presence or absence of mussels) to examine intra-annual variation in the effects of wave action, starvation, and prey availability on the proportion of sea stars that reached the top of the mounds. We treated this analysis as a particular case of the generalized linear model to correct for heteroscedasticity and deviation of residuals from normality detected in the first place with a classical linear model. We used a binomial distribution of the residuals because the response variable was a proportion (McCullagh and Nelder 1989; Bolker et al. 2008). No binomial variation was detected. Prior to running this four-way ANOVA, we used a one-way ANOVA (also with a binomial distribution) in each season with the factor Block (each daily block of one replicate of each treatment) to determine if the proportion of sea stars differed among blocks within each season. There was no significant effect of Block in winter (χ^2=5.70, p=0.840) and summer (χ^2=3.51, p=0.967), and hence we ran the four-way ANOVA on data pooled from all blocks. The four-way ANOVA was applied to the raw data (n=264).

We used a four-way ANOVA with the factors Season (winter and summer trials), Wave (null, low and high wave velocity), Starvation (fed and starved sea stars), and Prey (presence or absence of mussels) to examine intra-annual variation in the effects of wave velocity, starvation, and prey availability on the proportion of time that sea stars spent on

top of the mounds, whether they reached the top or not. Prior to running this four-way ANOVA, we used a one-way ANOVA in each season with the factor Block (each daily block of one replicate of each treatment) to determine if the proportion of time differed among blocks within each season. There was no significant effect of Block in winter ($F_{10,121}$=0.46, p=0.92) and summer ($F_{10,121}$=0.92, p=0.52), and hence we ran the four-way ANOVA on data pooled from all blocks. The four-way ANOVA was applied to the raw data (n=264).

Distribution and abundance of *A. rubens*: We used a one-way ANOVA with the factor Depth (2, 4, and 8 m) to examine the effect of depth on *A. rubens* density at BCC. The analysis was run on raw data pooled from all sampling dates (n=21). We then used multiple linear regression analysis to relate *A. rubens* density at each depth (2, 4, and 8 m) to sea temperature and wave height at BCC. Each regression model (three in total) was based on seven data points (n=7). Each point was the mean *A. rubens* density from the 10 frames of each pair of transects for a given depth and sampling date, and corresponding sea temperature and standardized (see below) significant wave height (SWH, the average height of the highest one-third of the wave data) averaged over the 48 hours preceding each sampling date (preliminary analysis showed stabilization of variation beyond 48 h). We used mean temperatures from the logger at the 3 m depth in the analyses of density at 2 and 4 m depths, and mean temperatures from the logger at 9 m in the analysis of density at 8 m. SWH is a proxy of wave energy at the top of a water column. It is commonly used, in the absence of velocity data, to relate ecological responses of benthic organisms, such as displacement and abundance, to the general wave environment (the higher the SWH, the higher the wave energy). However, wave energy,

and hence the effect of SWH on benthic organisms, attenuates with depth according to a logarithmic function that varies with wave period (Denny and Wethey 2001). We accounted for such attenuation by standardizing SWH data across depth as follows. We used raw SWH data in the analysis of sea star density at 2 m because of the relatively low attenuation of wave energy at this depth (Denny and Wethey 2001) and highest possible wave energy among the three depths sampled. However, for the analyses at 4 and 8 m, we used raw SWH data multiplied by the ratio of the theoretical maximum horizontal wave velocity at either depth to the theoretical maximum horizontal wave velocity at 2 m (our reference depth with the highest wave energy) for the characteristic wave period of 5 at our study site (see Figure 1.9 in Denny and Wethey 2001). The ratio at 4 and 8 m was respectively 0.9 and 0.4. Our approach to standardization of SWH is less precise than using velocity data, which were not available for the present study. However, it certainly is a better representation of the effects of attenuating wave energy with increasing depth on sea stars, than assuming no attenuation of wave energy with increasing depth. We used a one-way ANOVA with the factor Depth (2, 4, and 8 m) to examine differences in standardized SWH among depths (data pooled from all sampling dates, n=21). We treated this analysis as a particular case of the generalized linear model to correct for deviation of residuals from normality detected in the first place with a classical linear model. We used an inverse Gaussian distribution of the residuals with a canonical link because the data were right skewed and bounded to zero (Folks and Chikara 1978). Because we could not presume of the absence or presence of synergistic effects between the two explanatory variables (temperature and SWH), all analyses were conducted using the multiplicative error model approach, whereby explanatory variables are tested both for individual and

interactive effects (Kleinbaum et al. 2008). Accordingly, when interactive effects were not significant we presented models with individual effects of only those explanatory variables that were significant in the truncated model. The three analyses were applied to the raw data.

In all ANOVAs, MANOVAs, and regression analyses, homogeneity of the variance was verified by examining the distribution of the residuals. Normality of the residuals was verified by examining the normal probability plot of the residuals (Snedecor and Cochran 1989). To detect differences among levels within a factor (ANOVAs and MANOVAs), we used Tukey HSD multiple comparison tests (comparisons based on least-square means) (Sokal and Rohlf 2012). A significance level of 0.05 was used in all analyses, which were carried out with R 2.15.2. All means are presented with standard errors (mean ± SE) unless stated otherwise.

2.3. RESULTS

2.3.1 Experiment 1

Analysis of data from Experiment 1 indicated that the distance moved by *Asterias rubens* varied with season between levels of starvation (a significant interaction between the factors Season and Starvation, Table 2.2). Distance, which peaked to 175.9 ±10.8 cm in summer in fed sea stars, was >120% higher in summer than winter regardless of starvation (Figure 2.3). Starved sea stars displaced 20% less than fed sea stars in summer (LS means, p=0.0018), with no perceptible difference in winter (Figure 2.3). Wave velocity markedly affected displacement regardless of season and

Table 2.2. Summary of three-way ANOVA (applied to raw data) examining the effect of Season (summer and winter trials), Wave (null, low, and high wave velocity) and Starvation (fed and starved sea stars) on the distance moved by sea stars (*Asterias rubens*) in Experiment 1 (see Section 2.2.2 for a description of the experiment).

Source of variation	*df*	MS	F-value	*p*
Season	1	293937	193.80	<0.001
Wave	2	55742.5	36.75	<0.001
Starvation	1	11900	7.85	0.006
Season x Wave	2	3256.5	2.14	0.121
Season x Starvation	1	9067	5.98	0.016
Wave x Starvation	2	549.5	0.36	0.697
Season x Wave x Starvation	2	2401	1.58	0.210
Error	120	1516.7		
Corrected total	131			

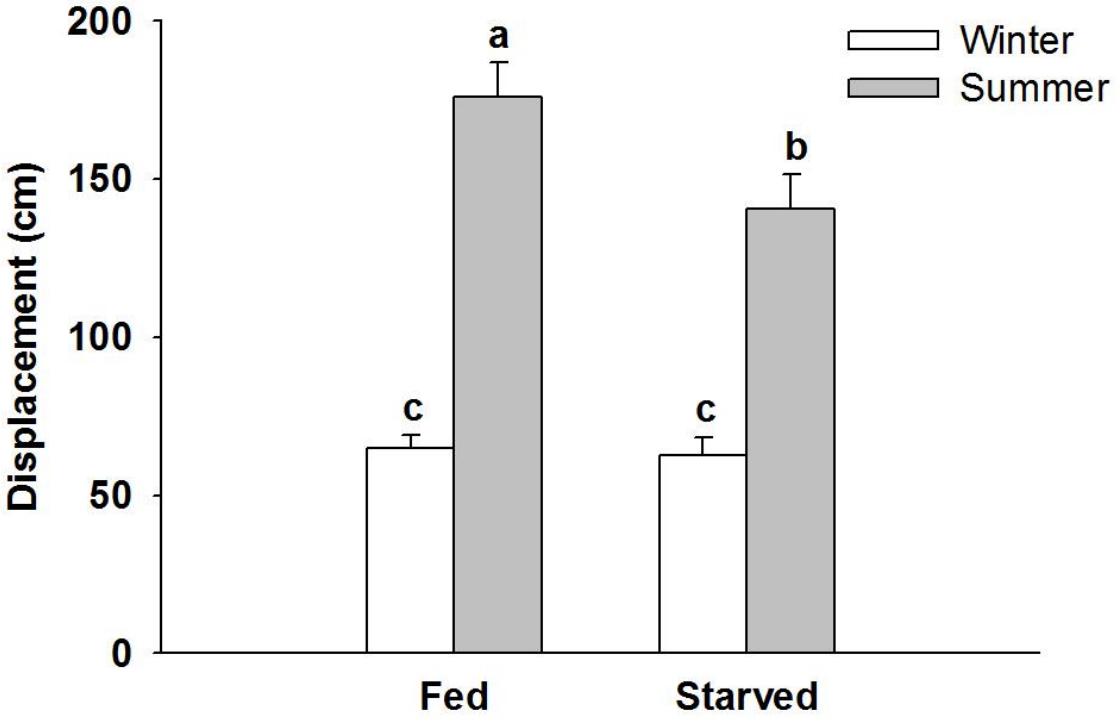

Figure 2.3. Mean (+SE) linear displacement of fed and starved sea stars (*Asterias rubens*) in winter and summer (Experiment 1). Data were pooled across Wave (null, low, and high wave velocity) treatments. Bars not sharing the same letter are different (LS means tests, $p<0.05$; n=33 for each combination of Season x Starvation).

starvation (Table 2.2), as shown by a decrease in distance of ~50% with an increase in wave velocity from null (142.7±11.0 cm) to high (75.5.±7.6 cm) (Figure 2.4). Furthermore, season and wave velocity, but not starvation, independently affected the proportion of time (POT) during which sea stars were dislodged (Table 2.3). POT was nearly twice higher in winter (7.9±2.0%) than summer (4.2±1.6%) and increased with wave velocity, being null in the absence of waves and five times higher at high (15.1±3.3%) than low (3.0±0.1%) velocity (Figure 2.4).

The MANOVA and associated univariate ANOVAs showed that season and wave velocity, but not starvation, independently affected the proportion of time (POT) that *A. rubens* spent in each of the six microhabitats (Tables 2.4 and 2.5). Overall, POT was highest on flat surfaces (>50% at any wave velocity) and lowest at the base of mounds (<2% at any wave velocity) (Figure 2.5). POT on flat surfaces was significantly higher at low (77%, data pooled across seasons) and high (86%) wave velocities than in the absence of waves (58%) (Table 2.5, Figure 2.5). Conversely, POT on the base of mounds and on protrusions (<6% at any wave velocity for both habitats) did not vary among wave velocities, but was at least two times higher in winter than summer (Table 2.5, Figure 2.5). POT in channels was consistently low (<6%) and did not vary significantly with season or wave velocity (Table 2.5, Figure 2.5), whereas that on mounds was more than three times higher in the absence of waves than at low and high velocities (Table 2.5, Figure 2.5). Season and wave velocity significantly affected POT on the tank walls, with as little as 6% at high velocity to up to 22% in the absence of waves, and 9% and 17% in winter and summer, respectively (Table 2.5, Figure 2.5).

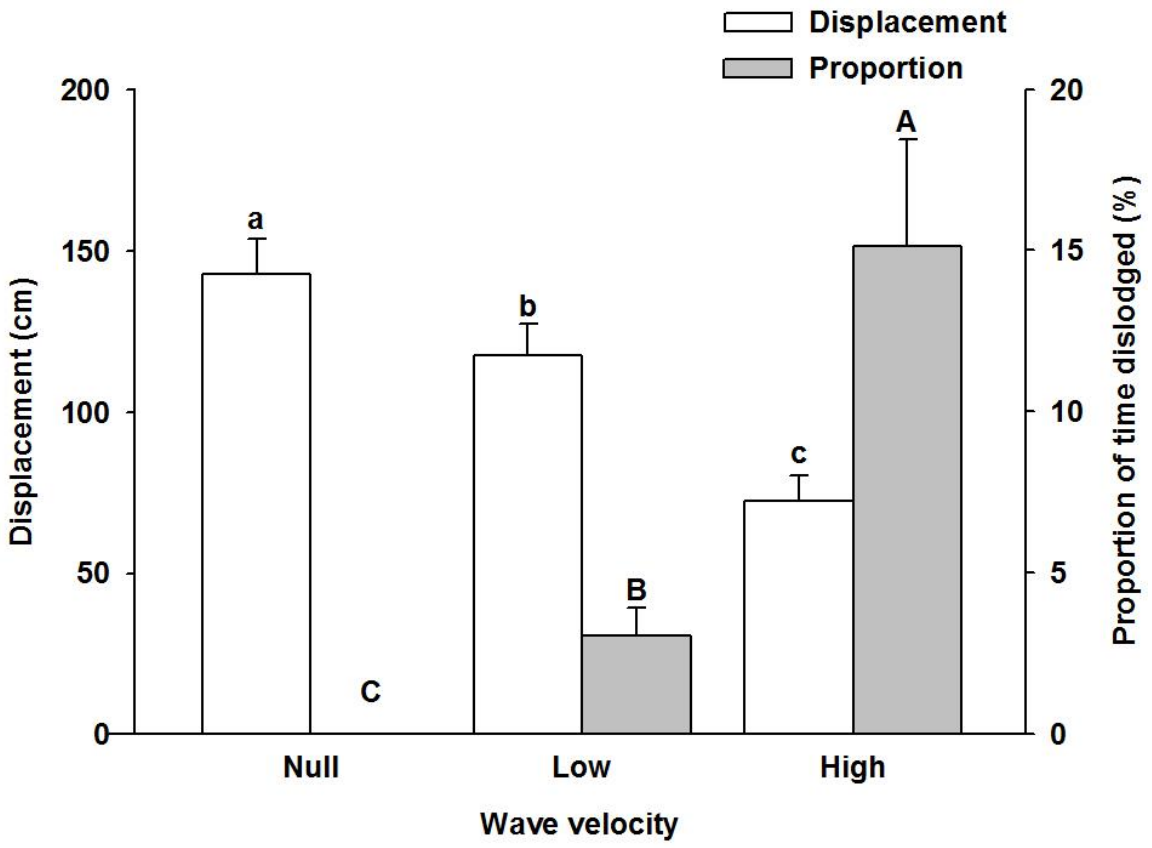

Figure 2.4. Mean (+SE) linear displacement of sea stars (*Asterias rubens*) and proportion of time during which sea stars were dislodged, at null, low, and high wave velocity (0.0, 0.1, and 0.2 m s^{-1}, respectively) (Experiment 1). Data were pooled across Season (winter and summer trials) and Starvation (fed and starved sea stars) treatments. Bars not sharing the same letter (small letters for displacement, capitals for proportion) are different (LS means tests, $p<0.05$; n=44 for each bar).

Table 2.3. Summary of three-way ANOVA (generalized linear model with binomial distribution, applied to raw data) examining the effect of Season (summer and winter trials), Wave (null, low, and high wave velocity) and Starvation (fed and starved sea stars) on the proportion of time during which sea stars (*Asterias rubens*) were dislodged in Experiment 1 (see Section 2.2.2 for a description of the experiment).

Source of variation	*df*	χ^2	*p*
Season	1	5.76	0.016
Wave	2	41.56	<0.001
Starvation	1	0.46	0.497
Season x Wave	2	5.89	0.053
Season x Starvation	1	0.50	0.481
Wave x Starvation	2	3.30	0.193
Season x Wave x Starvation	2	0.02	0.991

Table 2.4. Summary of three-way permutational MANOVA (applied to raw data) examining the effect of Season (winter and summer trials), Wave (null, low and high wave velocity) and Starvation (fed and starved sea stars) on the proportion of time spent by sea stars (*Asterias rubens*) in the six microhabitats in Experiment 1 (see Section 2.2.2 for a description of the experiment).

Source of variation	*df*	MS	F-value	*p*
Season	1	0.28	3.65	0.029
Wave	2	1.37	18.13	0.001
Starvation	1	0.04	0.52	0.658
Season x Wave	2	0.04	0.56	0.711
Season x Starvation	1	0.03	45.35	0.679
Wave x Starvation	2	0.16	2.19	0.068
Season x Wave x Starvation	2	0.05	0.71	0.595
Error	120	0.08		
Corrected total	131			

Table 2.5. Summary of two-way ANOVAs (applied to raw data) examining the effect of Season (winter and summer trials) and Wave (null, low and high wave velocity) on the proportion of time spent by sea stars (*Asterias rubens*) in the six microhabitats in Experiment 1 (see Section 2.2.2 for a description of the experiment).

Microhabitat	Source of variation	*df*	MS	F-value	*p*
Flat	Season	1	0.006	0.19	0.666
	Wave	2	0.876	28.68	<0.001
	Error	128	0.031		
	Corrected total	131			
Protrusion	Season	1	0.030	6.53	0.012
	Wave	2	0.003	0.73	0.485
	Error	128	0.005		
	Corrected total	131			
Channel	Season	1	0.001	0.12	0.726
	Wave	2	0.009	1.12	0.330
	Error	128	0.008		
	Corrected total	131			
Base of mound	Season	1	0.001	4.30	0.040
	Wave	2	<0.001	3.04	0.051
	Error	128	<0.001		
	Corrected total	131			
Mound	Season	1	0.025	2.64	0.106
	Wave	2	0.182	19.30	<0.001
	Error	128	0.009		
	Corrected total	131			
Wall	Season	1	0.213	9.23	0.003
	Wave	2	0.298	12.91	<0.001
	Error	128	0.023		
	Corrected total	131			

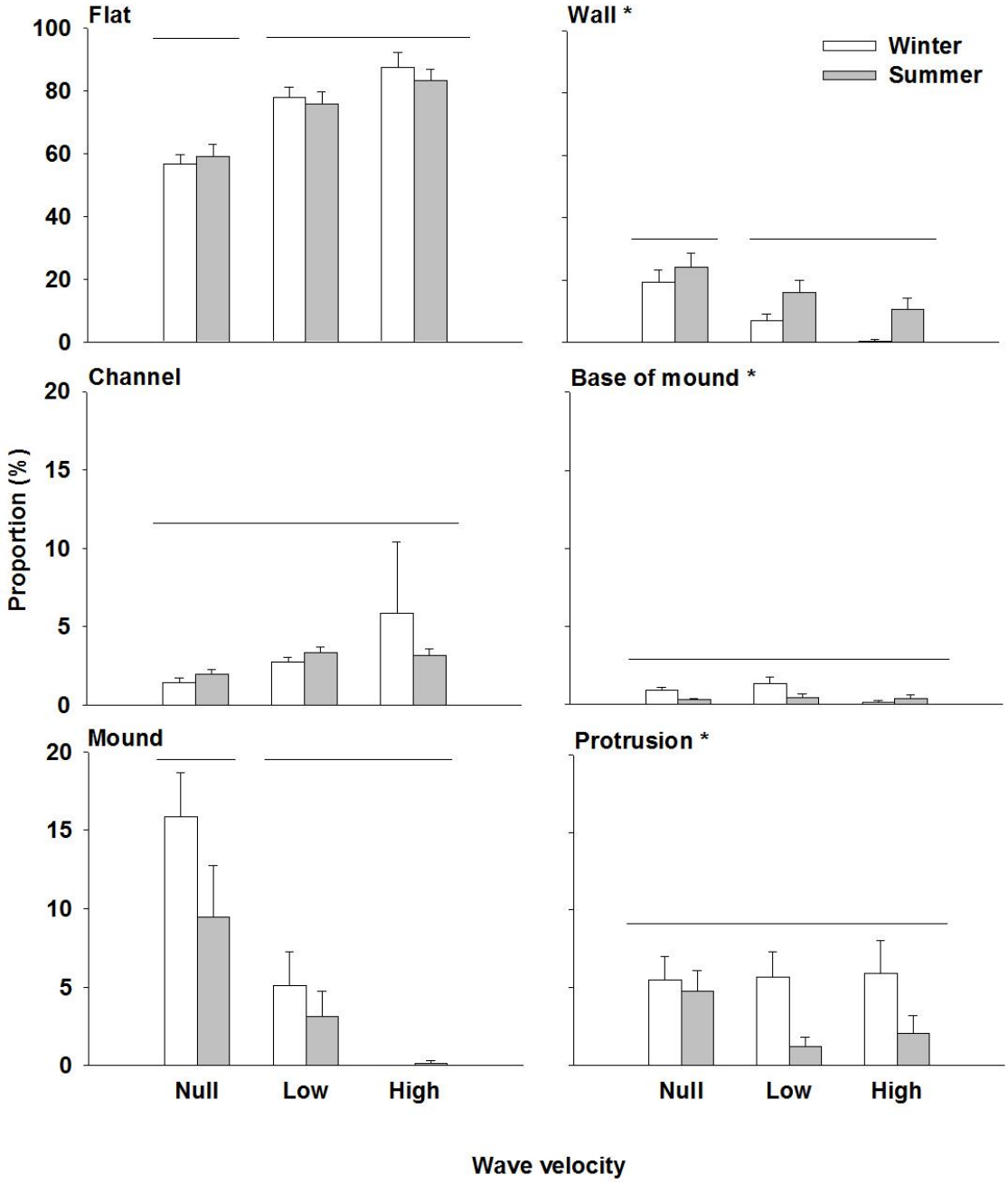
Flat
Wall *
Winter
Summer
Channel
Base of mound *
Mound
Protrusion *
Proportion (%)
100
80
60
40
20
0
20
15
10
5
0
Null
Low
High
Wave velocity

Figure 2.5. Mean proportion (+SE) of time spent by two sea stars (*Asterias rubens*) in each of six microhabitats at null, low, and high wave velocity (0.0, 0.1 and 0.2 m s^{-1}, respectively) in two seasons (winter and summer) (Experiment 1). Note the change in scale between the top two and bottom four panels. Wave treatments not bracketed by the same horizontal line are different (data pooled across Season and Starvation treatments, LS Means, $p<0.05$, n=44 for each velocity). Panels with an asterisk indicate a significant difference in proportions between seasons (winter>summer for protrusion and base of mounds, winter<summer for wall) (data pooled across Wave and Starvation treatments, LS means, $p<0.05$, n=66 for each season).

2.3.2 Experiment 2

Analysis of data from Experiment 2 indicated that season, wave velocity, and starvation, but not prey availability, independently affected the proportion of *Asterias rubens* that reached the top of the mounds (where wave velocity was highest in those treatments with waves and mussel prey, when present, were located) (Table 2.6). A higher proportion of sea stars reached the top in summer (76%) than winter (57%) (Table 2.6), when temperature averaged respectively 2.1°C and 13.4°C. Virtually all individuals (98%) reached the top in the absence of waves. However, this proportion markedly decreased with an increase in wave velocity, as shown by the 71% drop from null to high (Table 2.6, Figure 2.6). Significantly more starved (72%) than fed (61%) sea stars reached the top (Table 2.6).

The proportion of time (POT) that *A. rubens* spent on top of the mounds was influenced by a few interactive effects among season, wave velocity, prey availability, and starvation (significant Season x Prey, Season x Starvation, and Wave x Prey interactions, Table 2.7). POT in winter, which peaked to 25%, was not affected by prey availability, nor was it different from that in summer in the absence of prey (Figure 2.7). However, POT in summer was more than two times higher in the presence (45%) than absence (20%) of prey. POT was also at least 1.5 times higher in the presence of prey than in winter regardless of prey availability (Figure 2.7). Likewise, POT in winter, which peaked to 23%, did not differ between fed and starved sea stars, nor was it different from that in summer in fed individuals (Figure. 2.8). In summer it was ~1.5 times higher in starved (39%) than fed (25%) sea stars (Figure 2.8). POT decreased markedly with an

Table 2.6. Summary of four-way ANOVA (generalized linear model with binomial distribution, applied to raw data) examining the effect of Season (summer and winter trials), Wave (null, low, and high wave velocity), Prey (presence or absence of mussels) and Starvation (fed and starved sea stars) on the proportion of sea stars (*Asterias rubens*) that reached the top of the mounds in Experiment 2 (see Section 2.2.3 for a description of the experiment).

Source of variation	*df*	χ^2	*p*
Season	1	19.89	<0.001
Wave	2	121.19	<0.001
Prey	1	1.33	0.250
Starvation	1	6.22	0.013
Season x Wave	2	1.40	0.496
Season x Prey	1	0.10	0.750
Season x Starvation	1	1.20	0.273
Wave x Prey	2	4.65	0.098
Wave x Starvation	2	1.73	0.421
Prey x Starvation	1	0.05	0.819
Season x Wave x Prey	2	0.11	0.948
Season x Wave x Starvation	2	2.46	0.292
Season x Prey x Starvation	1	0.07	0.791
Wave x Prey x Starvation	2	0.25	0.881
Season x Wave x Prey x Starvation	2	0.80	0.669

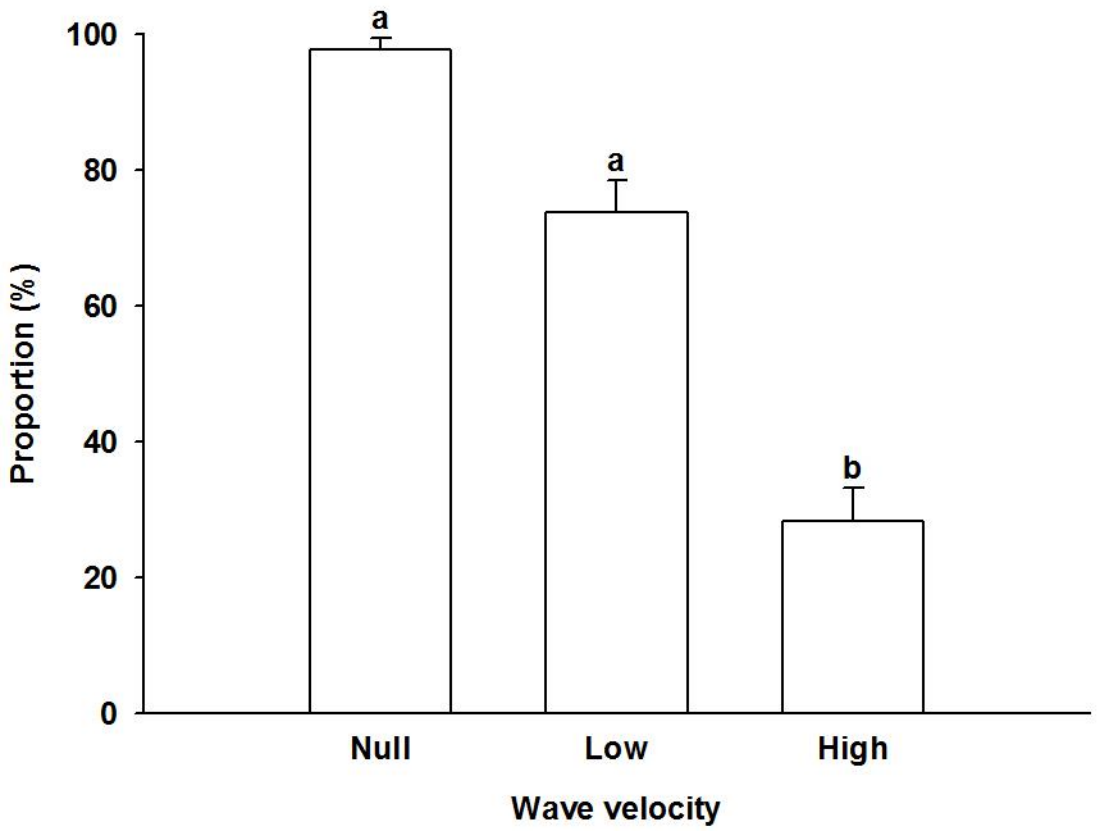

Figure 2.6. Mean (+SE) proportion of sea stars (*Asterias rubens*) that reached the top of the mounds at null, low and high wave velocity (0.0, 0.1 m and 0.2 m s^{-1}, respectively) (Experiment 2). Data were pooled across Season (winter and summer trials), Prey (presence or absence of mussels), and Starvation (fed and starved sea stars) treatments. Bars not sharing the same letter are different (LS means tests, $p<0.05$; n=88 for each wave velocity).

Table 2.7. Summary of four-way ANOVA (applied to raw data) examining the effect of Season (summer and winter trials), Wave (null, low, and high wave velocity), Prey (presence or absence of mussels), and Starvation (fed and starved sea stars) on the proportion of time sea stars (*Asterias rubens*) spent on top of the mounds in Experiment 2 (see Section 2.2.3 for a description of the experiment).

Source of variation	*df*	MS	F-value	*p*
Season	1	0.77	14.553	<0.001
Wave	2	5.78	54.850	<0.001
Prey	1	0.87	32.921	<0.001
Starvation	1	0.54	10.219	0.002
Season x Wave	2	0.02	0.142	0.867
Season x Prey	1	0.25	9.456	0.002
Season x Starvation	1	0.24	4.556	0.034
Wave x Prey	2	0.26	4.994	0.007
Wave x Starvation	2	0.29	2.787	0.064
Prey x Starvation	1	0.04	1.680	0.196
Season x Wave x Prey	2	0.02	0.333	0.717
Season x Wave x Starvation	2	0.16	1.537	0.217
Season x Prey x Starvation	1	0.07	2.667	0.104
Wave x Prey x Starvation	2	0.13	2.485	0.085
Season x Wave x Prey x Starvation	2	0.05	0.941	0.392
Error	240	0.05		
Corrected total	263			

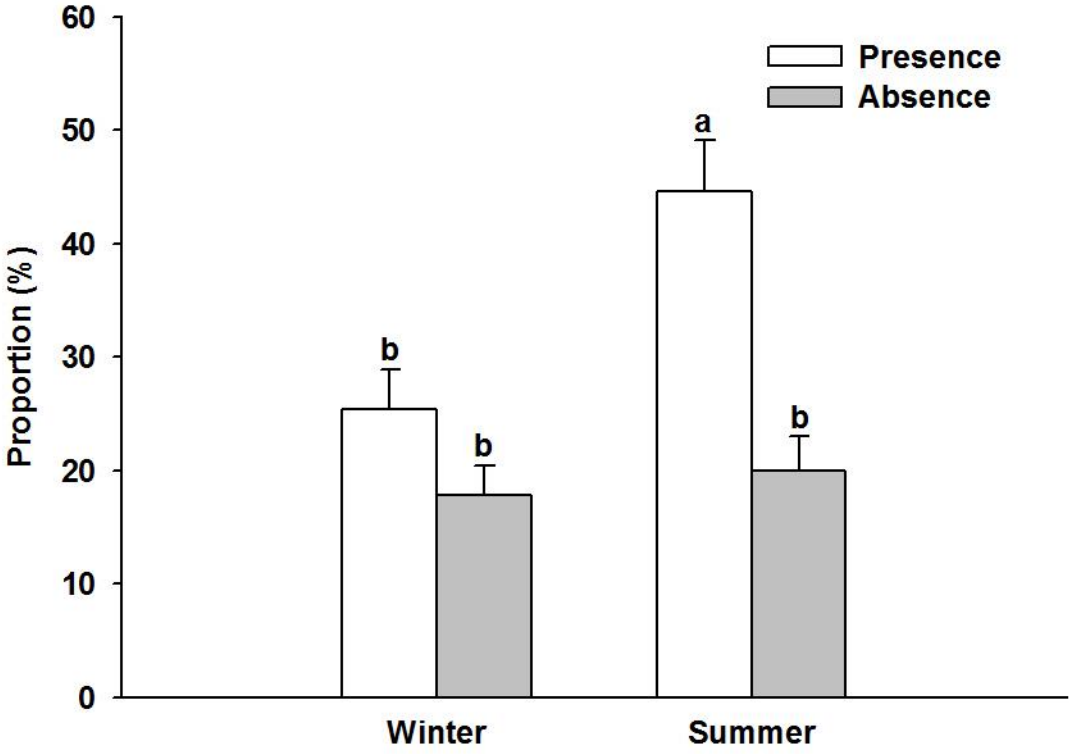

Figure 2.7. Mean (+SE) proportion of time spent by one sea star (*Asterias rubens*) on top of the mounds in two seasons, winter and summer, in the presence or absence of mussel (*Mytilus edulis*) prey (Experiment 2). Data were pooled across Wave (null, low, and high wave velocity) and Starvation (starved and fed sea stars) treatments. Bars not sharing the same letter are different (LS means tests, $p<0.05$; n=66 for each combination of Season x Prey).

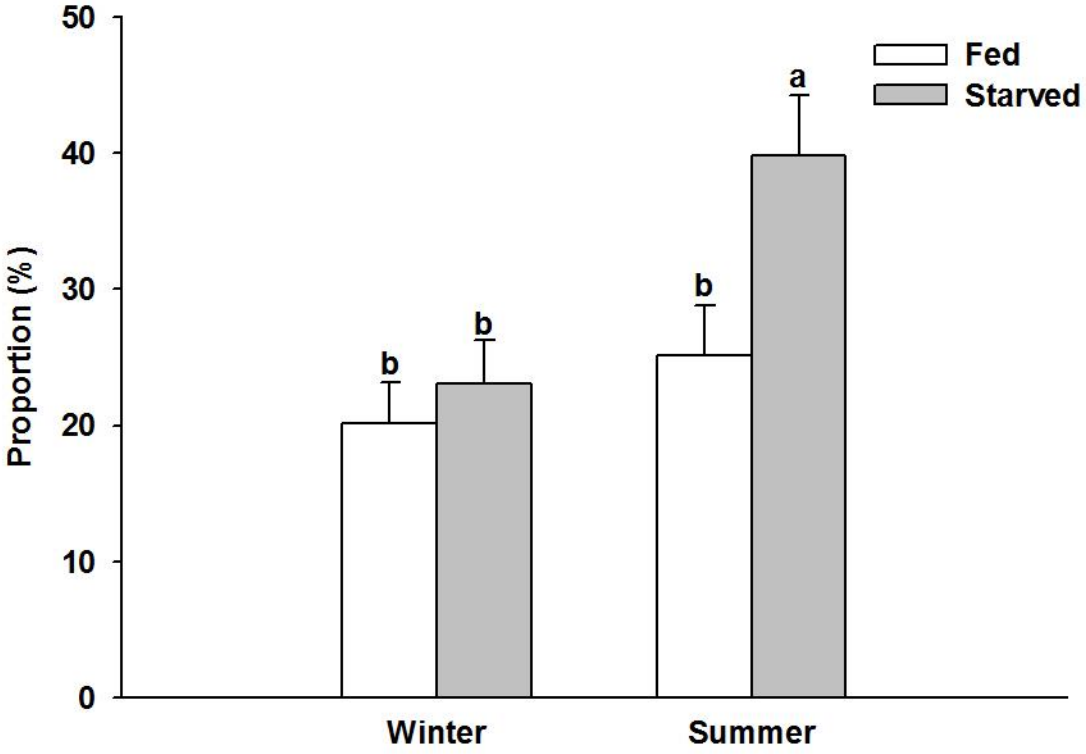

Figure 2.8. Mean (+SE) proportion of time spent by fed and starved sea stars (*Asterias rubens*) on top of the mounds in winter and summer (Experiment 2). Data were pooled across Prey (presence or absence of mussels) and Wave (null, low, and high wave velocity) treatments. Bars not sharing the same letter are different (LS means tests, $p<0.05$; n=66 for each combination of Season x Starvation).

increase in wave velocity from null (where it peaked to 55%) to high, both in the presence and absence of prey (Figure 2.9). It was 1.5 and 2.5 times higher in the presence than absence of prey at null and low intensity, respectively, and equally low (<11%) at high velocity with and without prey (Figure 2.9).

2.3.3 Distribution and abundance of *A. rubens*

Density of *Asterias rubens* at 2, 4, and 8 m depths at BCC from late April to mid-October 2011 ranged from 0 individuals m^{-2} at 2 and 4 m on several sampling dates, to 1.8±0.4 individuals m^{-2} at 8 m (on 13 October). It differed among depths (Table 2.8), being >4 times higher at 8 m than at 2 and 4 m (Figure 2.10). Temperature dropped to 0.9°C at 4 m on 23 April and peaked to 11.3°C at 2 m on 23 August. It varied consistently among the three depths, averaging 7.0±1.4, 6.8±1.3, and 6.7±1.3°C at 2, 4, and 8 m, respectively. Raw significant wave height (SWH) ranged from 0.11 m on 23 September to 0.56 m on 13 October, averaging 0.26±0.06 m. Multiple linear regression analysis showed that *A. rubens* density was not related to temperature and standardized SWH at 2 m [$F_{(2,4)}$=1.056, p=0.43] and 8 m [$F_{(2,4)}$=3.616, p=0.13]. However, density was positively related to standardized SWH, but not to temperature, at 4 m (Figure 2.11). Standardized SWH did not differ between 2 and 4 m and was comparatively 50% lower at 8 m (one-way ANOVA [generalized linear model, see Section 2.2.5]: Factor=Depth, χ^2=9.80, p=0.007).

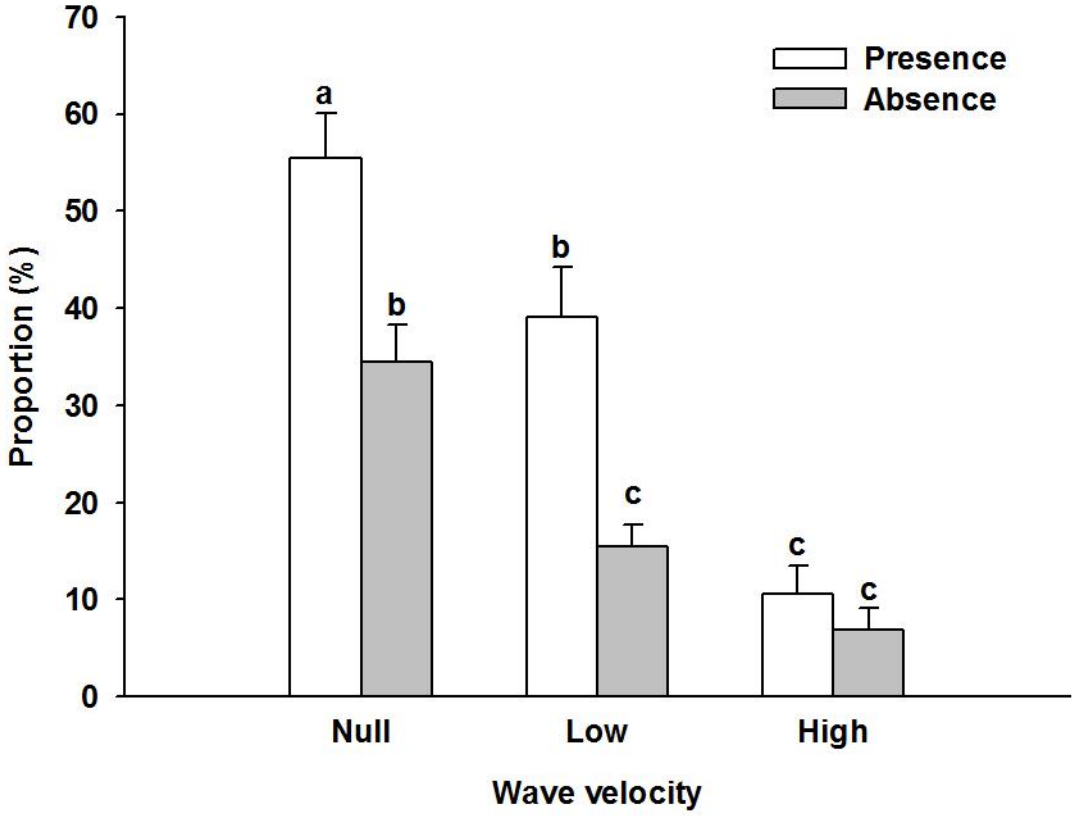

Figure 2.9. Mean (+SE) proportion of time spent by one sea star (*Asterias rubens*) on top of the mounds at null, low, and high wave velocity (0.0, 0.1, and 0.2 m s^{-1}, respectively) in the presence or absence of mussel (*Mytilus edulis*) prey (Experiment 2). Data were pooled across Starvation (starved and fed sea stars) and Season (winter and summer trials) treatments. Bars not sharing the same letter are different (LS means tests, $p<0.05$; n=44 for each combination of Wave x Prey).

Table 2.8. Summary of one-way ANOVA (applied to raw data) examining the effect of Depth (2, 4 and 8 m) on the density of sea stars (*Asterias rubens*) on the seabed at Bread & Cheese Cove from 23 April to 13 October, 2011.

Source of variation	*df*	MS	F-value	*p*
Depth	2	1.13	10.08	0.001
Error	18	0.12		
Corrected total	20			

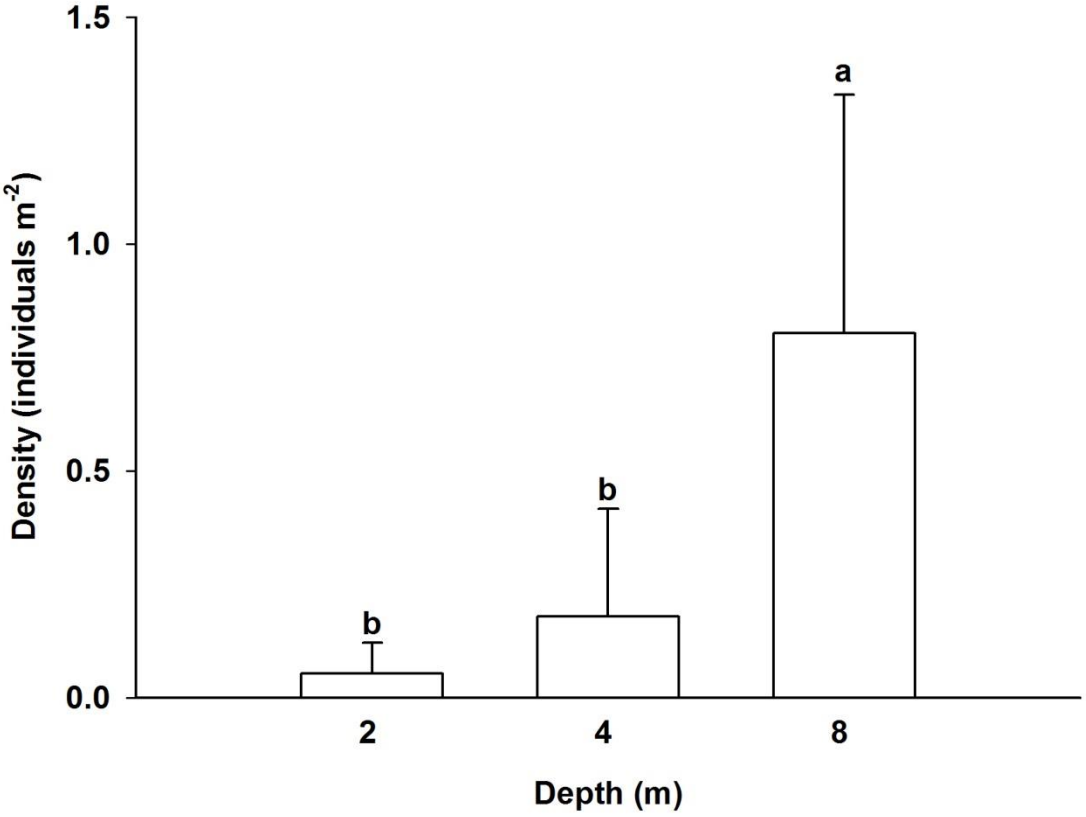

Figure 2.10. Mean (+SE) density of sea stars (*Asterias rubens*) at three depths at Bread & Cheese Cove from 23 April to 13 October, 2011. Bars not sharing the same letter are different (LS means tests, $p<0.05$; n=7 at each depth).

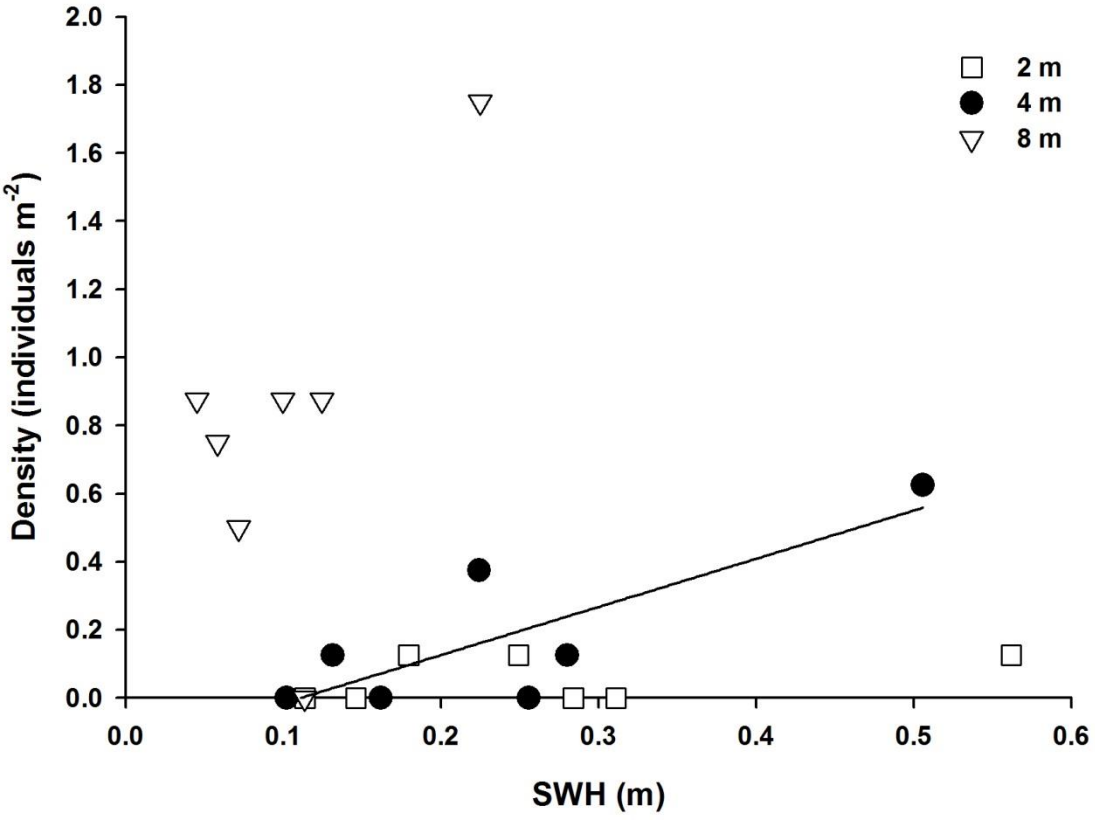

Figure 2.11. Relationship between the density of sea stars (*Asterias rubens*) and standardized significant wave height (SWH) at 2, 4, and 8 m depths at Bread & Cheese Cove from 23 April to 13 October, 2011 (see Section 2.2.5 for details of standardization of SWH data). The line is the linear fit to the raw data at 4 m (Density = -0.157 + 1.415 SWH; r^2=0.647, p=0.029, n=7 at each depth).

2.4. DISCUSSION

Our study demonstrates that wave action is a key determinant of displacement, habitat selection, and the ability to contact mussel (*Mytilus edulis*) prey in *Asterias rubens* from southeastern Newfoundland. A first indication of this is provided by our finding, in Experiment 1, that sea stars in the oscillatory wave tank displaced up to 50% less with an increase in wave velocity from null (0.0 m s^{-1}), to low (0.1 m s^{-1}), to high (0.2 m s^{-1}), regardless of season (winter versus summer) and starvation (fed versus 3-week starved individuals). Such a decrease is consistent with the finding by Gagnon et al. (2003) that *A. rubens* from the northern Gulf of St. Lawrence displaced two times more in the absence of waves than in the presence of oscillatory waves with a slightly higher peak velocity of 0.3 m s^{-1}. The decrease in displacement in the present study was gradual, with no sharp drop (threshold) over the range of velocities tested. Yet, sea stars detached from the bottom and were rocked by waves 15% and 3% of the time at high and low velocities, respectively. These results suggest that the majority of individuals can adapt relatively easily to characteristic water flows in their natural habitats (D'Amours and Scheibling 2007, P. Gagnon and K. Millar, unpublished data) by reducing displacement and the risk of dislodgement.

We conducted Experiment 1 and Experiment 2 in winter (February and March) and summer (September and October) of the same year. This was done to test the prediction that displacement, frequency of association with topographically uneven microhabitats, and the ability to contact prey differ between seasons. We had targeted these seasons because of marked differences in sea temperature, ~2°C in winter and ~13°C in summer,

and the underlying opportunity to interpret results on the basis of such a marked temperature difference. While temperature was confounded by time (season), it is arguably a better representation of likely seasonal variation in sea star behavior. Indeed, other environmental factors such as day length, salinity, and the concentration of oxygen in the water column change with season (Pinet 2011). However, it is widely acknowledged that temperature is the primary factor that affects metabolism, and ultimately behavior, of ectothermic organisms like *A. rubens* in natural habitats (Gillooly et al. 2001; Brown et al. 2004b; Harley 2013). Matheson and Gagnon (2012b) used a similar approach to investigate effects of temperature on foraging in rock (*Cancer irroratus*) and green (*Carcinus maenas*) crabs from southeastern Newfoundland. Below we cautiously interpret results as they relate to possible temperature effects.

We found that displacement in *A. rubens* was substantially higher (by 120%) in summer than winter, regardless of starvation, but lower in starved than fed individuals in summer only. These findings have several conceptual implications. Firstly, they suggest that water temperature markedly affects the ability of the sea star to explore its environment, which is a critical step for feeding, especially when prey resources vary in space and time (Himmelman 1984, 1991; Gaymer et al. 2001b; Witman and Dayton 2001). This is consistent with the notion that the ability of *A. rubens* to compete is lower in winter, when temperature is low, than in summer (Gaymer and Himmelman 2013). Secondly, it suggests that food deprivation in warm water further decreases the likelihood of encounters between *A. rubens* and prey. Such decrease would put the sea star at a higher risk of not being able to cope with the generally higher metabolic demand imposed on ectothermic organisms as temperature increases (Gillooly et al. 2001; Brown et al.

2004b). That nearly twice more sea stars were dislodged in winter than summer further supports the notion that *A. rubens* is biomechanically sensitive to the thermal environment, with increased vulnerability to high water flows in the cold and generally wavier winter months (Lauzon-Guay and Scheibling 2007; Scheibling and Gagnon 2009).

Our study of the proportion of time (POT) that *A. rubens* spent in each of six microhabitats in Experiment 1 supported our prediction that the frequency of association with topographically uneven microhabitats is generally higher in winter than summer. Starvation, however, had no perceptible effect on POT, indicating that the association with a particular microhabitat was decoupled from hunger state. Interestingly, sea stars predominantly stayed on flat horizontal surfaces and they did so more frequently in the presence than absence of waves. Besides, POT in each of the two most uneven microhabitats, protrusions and base of mounds, was significantly higher in winter than summer but did not differ among wave treatments. The latter result indicates that sea stars are generally more inclined to establish contact with surfaces that exhibit sharp angles and provide a good purchase at a time of year when temperature is low and wave action, high. Such structurally complex surfaces could locally reduce hydrodynamic forces, providing shelter. Altogether these results are consistent with our observations of a majority of *A. rubens* attaching firmly to small bottom irregularities in winter at multiple sites in southeastern Newfoundland, followed by gradual increase in displacement and transition to smoother and more vertical surfaces in spring and summer. We showed that significantly more sea stars climbed on the relatively smooth and vertical walls of the wave tank in summer than winter, as well as in the absence than presence of waves regardless of velocity. The latter result further suggests that *A. rubens* balances the

benefits of displacement with the risk of being dislodged, and does so in a particularly conservative way in winter. Interestingly, we found that one of the sharpest declines in POT with an increase in wave velocity was in the mound microhabitat, with a two-order-of-magnitude decrease from null to high wave velocity. Because of its higher position in the water column, peak water velocity in the mound microhabitat was at least 50% higher than in any of the five other microhabitats in both low and high wave velocity treatments. The latter finding indicates that *A. rubens* uses this kind of microhabitat parsimoniously, probably to minimize the risk of dislodgement.

Results of Experiment 2 are consistent with the notion conveyed by Experiment 1 that prey on topographically high points are increasingly less accessible to *A. rubens* as wave action increases, therefore providing mussels with a spatial refuge against predation as proposed in other studies (Menge and Lubchenco 1981; Witman and Grange 1998; Gagnon et al. 2003). Consistent with our predictions, significantly more sea stars that left the centre of the depression reached the top of the surrounding mounds 1) in summer than winter, 2) in the absence than presence of [high velocity] waves, and 3) when starved than fed. However, we also found that similar numbers of sea stars reached the top of mounds, whether there were prey or not on the top. The latter result reinforces the suggestion from Experiment 1 that topographically high points are a particularly challenging component to habitat exploration in *A. rubens*, especially in wavy conditions. Sea stars in Experiment 2 were initially restricted to a relatively small area (centre of the depression, <0.1 m^2) and they could only leave it by moving to the top of mounds. The greater displacement of sea stars in summer than winter (Experiment 1), together with the potential benefits of

exploring a greater area, could explain in part why more sea stars reached the top of mounds in summer, regardless of the presence or absence of mussels.

Distance chemodetection is common among sea stars (Smith 1940; Feder and Christensen 1966; Zafiriou 1972; Rochette et al. 1994). Gagnon et al. (2003) provided the first experimental demonstration that *A. rubens* can use distance chemodetection to localize mussel prey under conditions of back-and-forth flows similar to those in the present study. Mussels and *A. rubens* were aligned horizontally in the latter study (Gagnon et al. 2003), whereas in the present study mussels were located on topographically higher points than *A. rubens*. Accordingly, our finding that similar numbers of sea stars reached the top of mounds, whether there were prey or not on the top, also suggests that *A. rubens* has limited capacity in detecting and pursuing prey that are located on topographically higher points than itself, at least under conditions of back-and-forth flow. On flat surfaces, *A. rubens* and *Leptasterias polaris* normally displaces cross-current in search of prey (Rochette et al. 1994; Drolet and Himmelman 2004). Adding a third vertical dimension to the hydrodynamic and chemical environment and forcing *A. rubens* to make contact with a physical barrier (base of mounds) may decrease its ability to determine the direction to take to find prey. This may be especially true in small topographic depressions where vertical displacement is required to detect chemical gradients. Alternatively, the water in the wave tank (closed system) may have saturated with chemicals released by mussels, which may blur the spatial and temporal definition of odour plumes to undetectable levels. We believe that the later situation was unlikely given the very large volume of water (~1600 L) in the tank. We found that sea stars that

reached the top of mounds spent significantly more time there 1) in the presence than absence of mussels in summer only, 2) when starved than fed in summer only, and 3) in the presence than absence of mussels at null and low wave velocities [it was equally low at high velocity with and without prey]. The first two results indicate that *A. rubens* is generally more sensitive to the presence of prey at a time of year when displacement and metabolism, and hence energetic requirements, are high (Gillooly et al. 2001; Brown et al. 2004b). The latter result again demonstrates the pervasive effect of increased wave action on *A. rubens*, while indicating that the presence of prey can increase the tolerance of the sea star to intermediate water flows.

Our study of variation over six months (late April to mid-October, 2011) in the abundance of *A. rubens* at Bread and Cheese Cove (BCC) indicated that the sea star occurred in relatively low numbers across the 2-to-8-m depth range, on average ~0.3 individuals m^{-2}. This figure is lower than the typical density of ~1-2 individuals m^{-2} in the Mingan Islands, in the northern Gulf of St. Lawrence (Himmelman and Dutil 1991; Gaymer et al. 2001a; Gaymer and Himmelman 2002). Gaymer et al. (2001a) found that the abundance of *A. rubens* in June and August in three consecutive years at Petite Ile au Marteau (in the Mingan Islands), peaked in the first 3 m of water where a mussel bed had developed. Densities were low and uniform below 3 m. However, they found the opposite pattern at a nearby site, Ile aux Goélands, where a mussel bed was also present in the first 3 m: low densities of *A. rubens* in the first 3 m, followed by a gradual increase in numbers with depth to a maximum at 11 to 13 m (Gaymer et al. 2001a). The authors attributed these opposite patterns mainly to competitive interactions between *A. rubens* and

L. polaris, and higher abundance of *A. rubens*' second most preferred prey (the ophiuroid *Ophiopholis aclueata*) in shallow water at the former site (Gaymer et al. 2001a). Patterns of distribution of *A. rubens* at BCC paralleled those at Ile aux Goélands, with >4 times more individuals at 8 m than at 2 m and 4 m. However, mussels at BCC were relatively rare throughout our 6-month survey, with only a few isolated patches in the first 2 m, below the kelp (*Alaria esculenta*) canopy. Likewise, ophiuroids and other potential prey, as well as *L. polaris*, were virtually absent from the site. It therefore appears that intraspecific competition and prey availability were unlikely to explain the observed pattern of *A. rubens* distribution at BCC. As explained below, our results suggest that the hydrodynamic environment contributed to this pattern.

Standardized significant wave height (SWH), which we used as a proxy for the effects of attenuating wave energy with increasing depth on sea stars, did not differ between 2 m and 4 m and it was comparatively twice lower at 8 m. Yet, density of *A. rubens* was positively related to standardized SWH at 4 m only (no significant relationships at 2 m and 8 m). That *A. rubens* density increased with standardized SWH at 4 m but not at 2 m, despite similar standardized SWH between these depths, suggests *A. rubens* migrated from greater depths (e.g. 8 m) where it was more abundant. As discussed above, our two experiments in a wave tank environment established that displacement in *A. rubens* generally decreases with an increase in wave velocity from 0 to 0.2 m s^{-1}. The majority of sea stars still displaced relatively easily at 0.2 m s^{-1}, indicating that the maximum wave velocity at which *A. rubens* can displace should be well above the latter value. Accordingly, we suggest that flow velocities at 2 m and 4 m at BCC were generally within or slightly above the range of velocities tested in the laboratory, and

sufficiently high to discourage further progression of *A. rubens* to shallower depths. Several studies have reported migrations of *Asterias* spp. to shallow water mussel beds in summer and to greater depths to avoid harsh conditions in winter (Pabst and Vicentini 1978; Menge 1982; Himmelman 1991; Gaymer et al. 2001a). Our results support the notion that *A. rubens* can migrate to shallower water.

In a concurrent study carried out over the same period as in the present study, Blain and Gagnon (2014) examined the persistence and temporal variation in epifaunal assemblages in three grazing-resistant, canopy-forming seaweeds (*Desmarestia viridis, Desmarestia aculeata* and *Agarum clathratum*) in the urchin barrens at BCC and one adjacent site, Keys Point. They documented a dramatic recruitment pulse in *A. rubens*' prey, such as bivalves (including *Mytilus edulis*) and gastropods, that occurred in October at both sites (Blain and Gagnon 2014). This pulse coincided well with the highest standardized SWH at 4 m at BCC noted in the present study. Accordingly, it is possible that the sudden influx of juvenile prey in the system towards the end of our survey, together with increased mixing of waterborne odours from these prey, triggered the bulk of the proposed migration of *A. rubens* from 8 m to 4 m. Density of *A. rubens* at BCC was unrelated to sea temperature at each of the three depths despite a difference of >10°C between highest and lowest temperature values. Sea temperature therefore had no perceptible effect on the vertical distribution of the sea star from early spring to early fall, which together with our other results reinforces the idea that the hydrodynamic environment plays a key role in the ecology of *A. rubens*.

Our study provides the first detailed examination of the mechanistic underpinnings of variation in displacement, microhabitat selection, and ability to contact prey in the common sea star, *Asterias rubens*. We conclude that wave action, and to a lesser extent starvation, are key modulators of the sea star's inclination and ability to explore its environment and localize prey. In southeastern Newfoundland, the response of *A. rubens* to wave action and starvation is adaptable, being generally stronger in summer than winter, when sea temperature differs markedly. Collectively, our findings speak to the importance of considering the wave environment in studies of sea star ecology. Further studies should attempt to investigate the full spectrum of abiotic and biotic factors that control the behavioral repertoire and feeding ecology of this functionally important consumer to better anticipate and predict the trophic cascade that altered sea state predicted to result from climate change, may trigger.

CHAPTER III

The role of temperature, body size, starvation, and potential competitor cues in mediating feeding in the common sea star, *Asterias rubens*

3.1. INTRODUCTION

A key aspect of the feeding ecology of specialist predators is the ability to switch to alternative prey or suboptimal-sized prey during competitive interactions, when prey abundance is limiting, or when environmental conditions adversely affect predators (Charnov 1976; Krebs 2001; van Baalen et al. 2001; Calcagno et al. 2014). Prey size and predator physiology can markedly affect consumption of a predator, especially when the prey has hard body parts that require longer handling time, and hence higher predator energy expenditure (Hughes and Elner 1979; Barbeau and Scheibling 1994b; Norberg and Tedengren 1995; Matheson and Gagnon 2012b). Because biological rate processes generally scale positively with increasing temperature, body size, and food intake, ectothermic predators should be increasingly sensitive to the thermal environment and food deprivation (starvation) as they grow larger (Brockington and Clarke 2001; Gillooly et al. 2001; Brown et al. 2004b). Intra-annual variation in temperature and prey abundance is typically high in high-latitude, seasonal seas (Menge and Sutherland 1987; Witman and Dayton 2001; Caines and Gagnon 2012), where ocean climate change and associated impacts on marine organisms are currently among the highest (Halpern et al. 2008; Burrows et al. 2011). Studying plasticity in prey consumption and size selection of functionally important, ectothermic, specialist predators is, therefore, essential to understand and predict drivers of alterations to northern reef communities.

The common sea star, *Asterias rubens* (formerly *Asterias vulgaris*, Clark and Downey 1992), is a major predator in the rocky subtidal zone in the northern Gulf of St. Lawrence and along the Atlantic coast of Newfoundland, Canada (Himmelman and Steele 1971; Gaymer et al. 2001a, b; Gaymer et al. 2004). In these regions, the sea star primarily

consumes bivalve prey with a strong preference for the blue mussel, *Mytilus edulis* (Gaymer et al. 2001b; Gaymer et al. 2004; Wong and Barbeau 2005). In the northern Gulf of St. Lawrence, small (12-16 cm in diameter), 1-week starved *A. rubens*: 1) mainly selects medium [15-30 mm in shell length] *M. edulis* when exposed to unlimited supplies of small, medium, and large individuals; and 2) reduces feeding without altering mussel size-selection in the presence of a major competitor, the northern sea star, *Leptasterias polaris* [Gaymer et al. 2001b, 2002]. The latter two studies, together with several others in eastern Canada (Himmelman and Dutil 1991; Barbeau and Scheibling 1994a; Gaymer et al. 2004), the Baltic Sea (Anger et al. 1977), the Wadden Sea (Aguera et al. 2012), and the North Sea (Hancock 1958) demonstrate that *A. rubens* is a highly selective predator even when prey abundance is limiting, while suggesting that feeding can vary seasonally. However, no study has specifically examined plasticity in prey consumption and size selection as it relates to temperature (but see Gaymer et al. 2002), prolonged (>1 week) starvation, and body size.

Knowledge about the feeding ecology of *A. rubens* in the predominantly cold waters of Newfoundland is sparse. It is limited to casual observations of aggregates of the sea star on prey (Himmelman and Steele 1971) and a recent study indicating that wave action and starvation modulate displacement, microhabitat selection, and ability to contact prey (*M. edilus*) in small [9-15 cm] individuals (Chapter II). The prevalence of the indigenous rock crab, *Cancer irroratus*, in Newfoundland subtidal communities (Matheson and Gagnon 2012b), together with rapidly increasing abundance of the invasive green crab, *Carcinus maenas* (DFO 2010), provide an opportunity to test effects of their presence on feeding in *A. rubens*. In southeastern Newfoundland, both crabs

occur in the same rocky habitats as *A. rubens* and they also feed readily upon *M. edulis* (Himmelman and Steele 1971; Matheson and Gagnon 2012a, b). Thus, both crabs qualify as potential competitors for *M. edulis* with *A. rubens*. Because *A. rubens* primarily uses chemodetection to locate prey and competitors (Castilla and Crisp 1970; Zafiriou et al. 1972; Gaymer et al. 2002; Drolet and Himmelman 2004), a logical starting point is to examine the effects of the "chemical presence" of both crabs on prey consumption and size selection in *A. rubens*.

In the present study, we use three laboratory experiments to test the effects of water temperature, body size, starvation, and chemical cues from potential competitors on mussel (*M. edulis*) consumption and size selection in *A. rubens* from southeastern Newfoundland. Specifically, we quantify 1) consumption of medium [15-30 mm] mussels by small [9-15 cm] sea stars fed or starved moderately [for three weeks] at three temperatures representative of middle-to-late summer highs [8, 11, and 15°C] and one temperature typifying late winter lows [2°C]; 2) consumption of small [5-15 mm], medium, and large [30-45 mm] mussels by small and large [25-30 cm] sea stars fed or starved moderately or severely [for six weeks]; and 3) consumption of small, medium, and large mussels by small sea stars starved moderately, in the presence or absence of chemical cues from *C. irroratus*, *C. maenas*, and crushed mussels [as an incentive to feed] [see Sections 3.2.1 to 3.2.4 for specific rationales and predictions].

3.2. MATERIAL AND METHODS

3.2.1. Collection and acclimation of organisms prior to experimentation

The three experiments in this study (Experiment 1, Experiment 2, and Experiment 3, see Sections 3.2.2 to 3.2.4) were conducted with *Asterias rubens* hand collected by divers in January, February, May, and August, 2013 at depths of 6 to 15 m from gently sloping bedrock platforms between Kings Cove (47°36'15.07" N, 52°52'55.17" W) and Lower Horse Cove (47°34'27.38" N, 52°54'13.38" W) in Conception Bay, Newfoundland (Canada). Sea stars were transported in large containers filled with seawater to the Ocean Sciences Centre (OSC) of Memorial University of Newfoundland. Upon arrival at the OSC (<6 hours after collection), the sea stars were transferred to 330-L holding tanks supplied with ambient flow-through seawater pumped in from a depth of ~5 m in the adjacent embayment, Logy Bay. We kept all 5-armed individuals that clung or displaced readily in the tanks, indicating normal activity. These sea stars were measured (length of the longest axis between two opposing arm tips, measured with a vinyl tape with a precision of 0.5 mm) to keep only those that fit either of two size classes: 9 to15 cm (hereafter "small"), for use in Experiments 1, 2, and 3, and 25 to 30 cm (hereafter "large"), for use in Experiment 2. We chose individuals in these size classes because 1) they are sexually mature (Nichols and Barker 1984; Himmelman and Dutil 1991), therefore eliminating variation in foraging from potential behavioral differences between mature and non-mature individuals, and 2) they were the most abundant at times of collection.

All sea stars used in the experiments were offered live blue mussels, *Mytilus edulis*, in the first three days of captivity to standardize hunger levels. They were then divided into three acclimation groups: "fed", "starved for three weeks", and "starved for six weeks". Fed sea stars were offered live *M. edulis* during the six weeks preceding

the trials. Sea stars starved for three weeks were offered live *M. edulis* during three weeks but were unfed during the following three weeks. Sea stars starved for six weeks were unfed during six weeks prior to experimentation. The three experiments were conducted over several weeks, which required that we create and maintain multiple groups of sea stars at various stages of starvation within the 330-L holding tanks. For small sea stars, this was done by isolating stars of a same acclimation group and designated week of usage in 10-L plastic container with eight to 10 individuals per container. Each container was covered with nylon netting of 1 mm mesh to prevent escape and allow water circulation. Large sea stars were too big for the containers, and hence were kept in 330-L holding tanks according to their acclimation group and designated week of usage, with 16 individuals per tank. Fed sea stars were offered mussels every three or four days. We removed empty mussel shells from each container and tank, and added respectively 100 to 150 and 200 to 250 mussels of 10 to 45 mm in shell length to provide continual access to mussel tissues.

Sea stars are generally tolerant to prolonged (>7 weeks) periods of starvation (Valentinčič 1973; McClintock and Lawrence 1985; Rochette et al. 1994). In *A. rubens*, a starvation of two to four weeks is long enough to initiate the release of reserve material from the pyloric caeca (Jangoux and van Impe 1977). However, a starvation of more than four weeks may trigger general autolysis ensuing from complete depletion of reserve material (Hancock 1958; Jangoux and van Impe 1977). Accordingly, we starved sea stars for three and six weeks to measure, as required, effects of moderate (three weeks) and severe (six weeks) starvation on prey consumption and prey size selection in *A. rubens* (see Sections 3.2.2 to 3.2.4). Mussels offered to the sea stars during the acclimation and

experiments were hand collected by divers at Foxtrap (47°30'47.51" N, 52°59'50.71" W) and Petty Harbour (47°27'50.78" N, 52°42'25.47" W). Rock crabs, *Cancer irroratus*, and green crabs, *Carcinus maenas*, used in Experiment 3 were collected in October 2012 with baited (herring) traps along wharves in Bay Bulls (47°18'49.35" N, 52°48'44.88" W) and North Harbour (47°51'00.63" N, 54°05'59.94" W), respectively. Rock and green crabs measured respectively 80 to 110 mm and 60 to 80 mm in carapace width, which is above the minimum size at sexual maturity in both species (Campbell and Eagles 1983; Audet et al. 2008). Only hard-shelled (non-molting) male crabs were used (females in both species were discarded at collection sites) to eliminate potential variation in chemical cues among crabs of different sexes, molting, and sexual stages. Mussels and crabs were transported in large containers filled with seawater to the OSC within six hours after collection, and kept separately in 330-L holding tanks supplied with ambient flow-through seawater. Crabs were offered mussels and pieces of salmon once a week prior to experimentation.

3.2.2. Temperature, starvation, and prey consumption (Experiment 1)

To quantify effects of water temperature and starvation on prey consumption, we used a factorial experiment (Experiment 1) in which small *Asterias rubens* fed or starved three weeks (see Section 3.2.1) were allowed to consume live blue mussels, *Mytilus edulis*, in seawater at three temperatures: 8, 11, and 15°C. Our primary objective was to examine feeding during the last few weeks of summer, when *A. rubens* increasingly moves towards, and aggregates on, shallow mussel beds in eastern Canada (Himmelman and Dutil 1991; Gaymer and Himmelman 2002; Gaymer et al. 2002). We

used 3-week starved sea stars because we were interested in the effect of moderate starvation and its interaction with temperature at a time of year when prey are relatively abundant (Gaymer et al. 2001a; Gaymer and Himmelman 2002) and most *A. rubens* are unlikely to exhibit more advanced starvation (see Section 3.2.1). We chose these temperature treatments because sea temperature in coastal Newfoundland, including the area where we collected *A. rubens*, typically peaks to 15-18°C in late August followed by a 5-10°C decrease until late September (Caines and Gagnon 2012; Blain and Gagnon 2013).

We carried out the experiment three times between 3 and 28 September, 2013 (hereafter termed "summer"). Trials lasted 90 h (preliminary trials showed demonstrable mussel consumption over this period), and were conducted in three adjacent water baths (GD120L; Grant). The volume of each bath enabled running simultaneously four replicates of each of the six experimental treatments. Temperature treatments were assigned randomly to each bath in each of the three experimental runs. On the first day of each run, four fed and four starved *A. rubens* were each introduced randomly to one of eight 1-L plastic containers in each bath pre-filled with seawater from the holding tanks. The eight containers in each bath formed a grid of 2 x 4. Mean daily water temperature in the holding tanks varied from 11.1 to 13.6°C (mean = 12.8±0.1°C). As a result, all sea stars underwent a change in temperature of 1.5 to 5.4°C. The largest changes, 4.5 to 5.4°C in 33% of trials, may qualify as a shock. However, they do occur in coastal Newfoundland in late summer, with frequent drops and rises of up to 8°C over the course of only a few hours to days (Caines and Gagnon 2012; Blain and Gagnon 2013). We did

not acclimate the sea stars to the experimental temperature treatments because 1) incorporating the natural thermal history of sea stars into trials was a more accurate representation of natural processes affecting sea star feeding over the short term, and 2) the variable thermal environment to which they were exposed prior to trials made it impossible to determine a proper acclimation time for each temperature treatment. Nevertheless, the water in each container was gradually cooled or warmed to the desired experimental temperature over the three hours that preceded the onset of each trial to facilitate the thermal transition of sea stars. Upon reaching the assigned temperature treatment, 25 live mussels of 15 to 30 mm in shell length were added to each container. Preliminary trials indicated that these mussel number and size class were sufficient to avoid complete depletion of mussels over 90 h. This mussel size class is also one of the preferred and readily consumed in small *A. rubens* (Gaymer et al. 2001b, 2002). At the end of each trial, we determined the number of mussels consumed by each sea star from the numbers of entirely eviscerated pairs of valves that had been dislocated from original pairs or were still attached. We used numbers of mussels consumed in each container to calculate the mean proportion of mussels (out of 25) consumed for each temperature and starvation treatment.

We carried out a shortened version of Experiment 1 three times between 8 March and 3 April, 2013 (hereafter termed "winter"), to test the prediction that feeding in *A. rubens* is higher in summer than winter and in starved than fed individuals. This prediction stems from the argument that the metabolic demand imposed on ectothermic organisms like *A. rubens*, and hence the necessity to feed, increases with temperature and presumably starvation (Jangoux and van Impe 1977; Hart and Chia 1990; Gillooly et al.

2001; Brown et al. 2004b). Sea temperature in southeastern Newfoundland is at a fairly stable annual minimum of 1-2°C from January to April (Blain and Gagnon 2013; Gagnon et al. 2013). Accordingly, in the winter trials we measured consumption of *M. edulis* by fed and 3-week starved *A. rubens* at one temperature only, 2°C. We used the same procedures as for the summer trials, except that each of the three winter runs was carried out with one water bath set at 2°C. Mean daily water temperature in the holding tanks varied from 1.2 to 2.5°C (mean = 1.8±0.1°C). All sea stars were thus exposed to small, and most likely inconsequential, changes in temperature of <0.8°C. Nevertheless, the water in each container was gradually cooled or warmed to 2°C during the three hours that preceded the onset of each trial to be consistent with the summer trials.

Each of the two (one temperature and two starvation levels) and six (three temperatures and two starvation levels) experimental treatments applied respectively in the winter and summer trials were replicated 12 times (four replicates in each of three runs in each season). In both winter and summer trials, a gentle stream of air bubbles was continuously injected in each container with aquarium pumps (Maxima, Hagen) to maintain oxygenation. Each trial was run with new sea stars and mussels.

3.2.3. Body size, starvation, and prey consumption and size selection (Experiment 2)

To quantify effects of body size and starvation on prey consumption and prey size selection, we used a factorial experiment (Experiment 2) in which small and large *Asterias rubens* fed or starved three or six weeks (see Section 3.2.1) were allowed to consume live *Mytilus edulis* in three size classes (shell length, in millimeters):

5-15 (small), 15-30 (medium), and 30-45 (large). We carried out the experiment during the first few weeks of summer, when *A. rubens* exhibits sustained feeding in eastern Canada (Gaymer and Himmelman 2002; Gaymer et al. 2004; Himmelman et al. 2005). We used sea stars of different size and starvation to test the prediction that mussel consumption is higher in large than small individuals, while increasing with duration of starvation. This prediction stems from the arguments that biological rate processes scale positively with increasing body size and presumably starvation (Jangoux and van Impe 1977; Gillooly et al. 2001; Brown et al. 2004b). We used 3- and 6-week starved sea stars because both starvation levels are likely at this time of year when *A. rubens* recovers from a prolonged (~five months) exposure to cold water at deeper over-wintering depths where mussels are largely absent (Himmelman and Dutil 1991; Blain and Gagnon 2013; Gagnon et al. 2013). We used mussels ≤45 mm because 1) *A. rubens* feeds primarily on mussels below this size (Gaymer and Himmelman 2002), and 2) most mussel beds accessible to *A. rubens* in southeastern Newfoundland are dominated by individuals below this size [P. Gagnon, personal observations]. We predicted that small *A. rubens* would select smaller mussels than large *A. rubens* and that the sea stars would be increasingly less selective as the duration of starvation increases, regardless of body size.

We carried out the experiment three times between 22 June and 11 July, 2013. Trials lasted 72 h, which was long enough for sea stars to consume a few but not all of the mussels as determined from preliminary trials. They were conducted in 75-L glass tanks (62 x 31 x 43 cm [L, W, H]) supplied with ~1 L min^{-1} of flow-through seawater. Water depth in each tank was ~40 cm. Each tank was surrounded by an opaque canvas to

eliminate light and visual stimuli from the lab. One incandescent, 100-watt light bulb (Soft White, Sylvania) located 45 cm above the water surface in each tank and controlled with rheostat and timer was used to create similar light conditions among tanks. We used a daily cycle of 16 h of light from 05h00 to 21h00 and 8 h of darkness from 21h00 to 05h00, consistent with the natural photoperiod at the time we ran the experiment. Each sea star in each tank was offered one aggregate of 60 mussels in the centre of the tank. Each aggregate consisted of 20 individuals in each size class (small, medium, and large) intermingled (to avoid clustering by size) in a Petri dish (10 cm in diameter). Aggregates were introduced to the tanks 15 minutes prior to the start of trials. Each trial began with the introduction to each tank of one sea star on top of the mussel aggregate. Sea stars were placed on the mussels to eliminate searching time had they been placed away from mussels, and hence provide each of them with the same amount of time (72 h) to consume mussels. At the end of each trial, we determined the number of mussels consumed by each sea star in each size class from the numbers of entirely eviscerated pairs of valves that had been dislocated from original pairs or were still attached. We used numbers of mussels consumed in each size class to calculate the mean proportion of mussels (out of 60) consumed for each sea star body size and starvation treatment.

Each of the six experimental treatments was replicated 12 times with four replicates in each of the three runs. In each run, the tanks were grouped in four blocks of six tanks each. Each tank in each block was randomly assigned to one of the six treatments. Tanks were scrubbed with towels, emptied, and filled with new seawater in the hours preceding each trial. Mean daily water temperature in the tanks varied from 6.9 to 11.5°C (mean = 8.9±0.05°C). Each trial was run with new sea stars and mussels.

3.2.4. Chemical cues and prey consumption and size selection (Experiment 3)

To quantify effects of chemical cues from potential competitors on feeding rate and prey size selection, we used an experiment (Experiment 3) in which small, 3-week starved *Asterias rubens* were allowed to consume live, intact *Mytilus edulis* in the same three size classes as in Experiment 2. Experiment 3 was performed in the presence or absence of cues from indigenous rock crabs, *Cancer irroratus*, invasive green crabs, *Carcinus maenas*, and crushed *M. edulis*. It was carried out during the first few weeks of summer with small, 3-week starved sea stars and mussels ≤45 mm for reasons given in Experiment 2.

Feeding of *A. rubens* upon (intact) *M. edulis* was assessed in six treatments: 1) the presence of rock crabs alone to quantify the effect of rock crab cue on *A. rubens* feeding, 2) the presence of rock crabs and crushed *M. edulis* to quantify the combined effect of rock crab and enriched prey cues on *A. rubens* feeding, 3) the presence of green crabs alone to quantify the effect of green crab cue on *A. rubens* feeding, 4) the presence of green crabs and crushed *M. edulis* to quantify the combined effects of green crab and enriched prey cues on *A. rubens* feeding, 5) the presence of crushed *M. edulis* alone to quantify the effect of enriched prey cue on *A. rubens* feeding, and 6) the absence of crabs and crushed *M. edulis* as a control. We tested the prediction that chemical cues from both crabs reduce mussel consumption without affecting mussel size selection in *A. rubens*. This prediction originates from the finding by Gaymer et al. (2002) that the presence of *Leptasterias polaris*, a major competitor of *A. rubens* in eastern Canada, reduces feeding in the latter without affecting prey size selection. We used crushed (with a hammer) *M.*

edulis in 50% of the treatments to test the complementary prediction that enriched prey cues offset the anticipated negative effect of crab cues on feeding in *A. rubens*.

We carried out the experiment three times between 26 June and 15 July, 2013. Trials, which lasted 72 h, were conducted in the same 75-L glass tanks and under the same light and water flow regimes as in Experiment 2. Each tank contained one small (~33% of the total tank space) and one large (~66% of the space) section separated by an opaque plastic divider inserted transversally in the tank (Figure 3.1). Water inflow and outflow were located respectively in the small (upstream) and large (downstream) sections. Each divider had eight perforations of 5 mm in diameter to let the water circulate from the upstream to downstream sections. The divider was stabilized with small weights at the bottom and tight enough on all sides to prevent displacement of organisms between sections (but see Section 3.2.5). Each sea star in each tank was offered one aggregate of 60 mussels in the centre of the downstream section. Each aggregate consisted of 20 individuals in each size class (small, medium, and large) intermingled (to avoid clustering by size) in a Petri dish (10 cm in diameter). Aggregates were introduced to the tanks 15 minutes prior to the start of trials. Three rock crabs or three green crabs, as well as 500±30 g of crushed *M. edulis* were also introduced to the centre of the upstream section 15 minutes prior to the start of trials in trials that necessitated one or the other. This amount of time was sufficient to allow chemical cues to diffuse across the tank as shown by preliminary trials with food dye in a concurrent study that used a similar tank setup (Matheson and Gagnon 2012b). When present, crushed mussels formed a thin layer that completely covered the bottom of the upstream

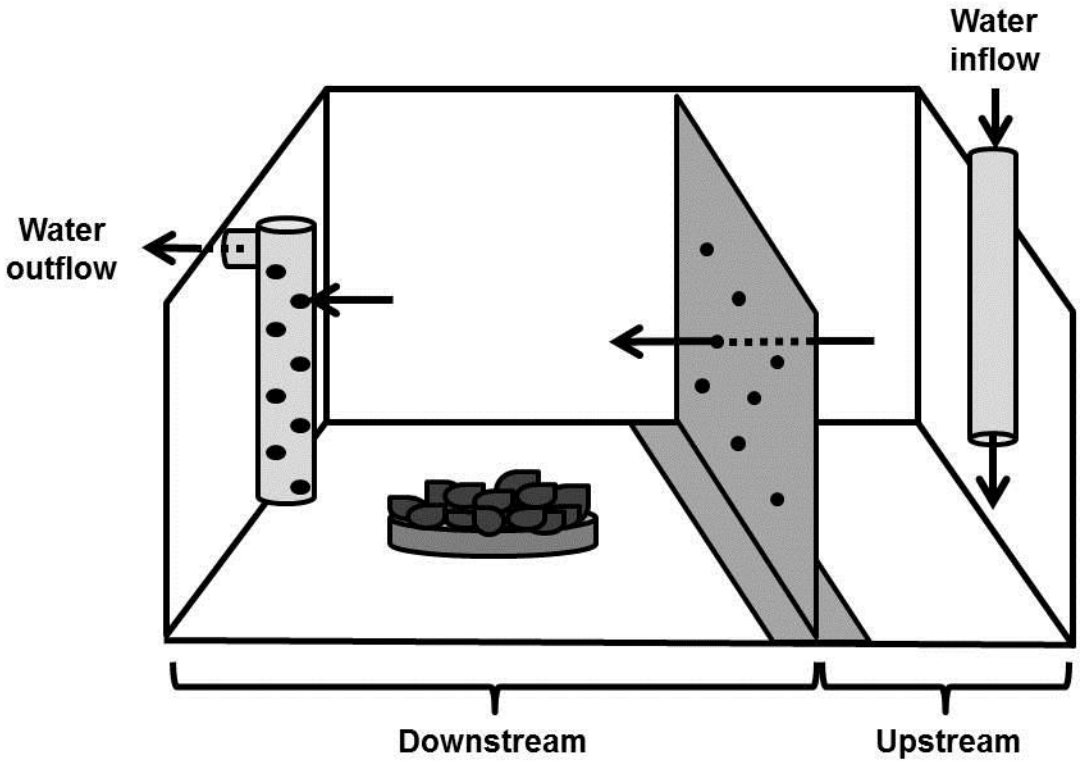

Figure 3.1. Representation (not to scale) of basic tank setup showing the relative position of water inflow, water outflow, mussel aggregate, and perforated plastic divider yielding one upstream and one downstream sections in the experiment quantifying effects of chemical cues from potential competitors on mussel (*Mytilus edulis*) consumption and size selection in the sea star *Asterias rubens* (Experiment 3). Arrows (→) indicate the direction of the water flow from entry in the tank (bottom of the inflow pipe), to across the divider, to exit from the tank (along and up to the top of the outflow pipe). Sea stars were always located in the downstream section. When present, crushed *M. edulis* and rock (*Cancer irroratus*) or green (*Carcinus maenas*) crabs were located in the upstream section (see Section 3.2.4 for more details).

section and upon which the crabs were feeding readily most of the time. Each trial began with the introduction to each tank of one sea star on top of the mussel aggregate. Sea stars were placed on the mussels for reasons given in Experiment 2. At the end of each trial, we determined the number of mussels consumed by each sea star from the numbers of entirely eviscerated pairs of valves that had been dislocated from original pairs or were still attached. We used numbers of mussels consumed in each size class to calculate the mean proportion of mussels (out of 60) consumed for each treatment.

Each of the six experimental treatments was replicated 12 times with four replicates in each of the three runs. In each run, the tanks were grouped in four blocks of six tanks each. Each tank in each block was randomly assigned to one of the six treatments. Tanks were scrubbed with towels, emptied, and filled with new seawater in the hours preceding each trial. Mean daily water temperature in the tanks varied from 6.5 to 11.6°C (mean = 9.3±0.05°C). Each trial was run with new sea stars and mussels.

3.2.5. Statistical analysis

Experiment 1: We used a two-way ANOVA with the factors Temperature (8, 11, and 15°C) and Starvation (fed or starved sea stars), to examine the effects of temperature and starvation on the proportion of mussels consumed by *Asterias rubens* during summer. We treated this analysis as a particular case of the generalized model to correct for heteroscedasticity and deviation of residuals from normality detected in the first place with a classical linear model. We used a binomial distribution of the residuals because the response variable was a proportion (McCullagh and Nelder 1989; Bolker et al. 2008). No

binomial variation was detected. Prior to running this two-way ANOVA, we used a one-way ANOVA (generalized linear model with a binomial distribution) with the factor Run (each of the three runs of four replicates of each treatment) to determine if results differed among runs. There was no significant effect of Run (χ^2=0.58, p=0.753), and hence we ran the two-way ANOVA on data pooled from all runs. One starved sea star died during one of the trials at 11°C. This data point was excluded from the analysis, yielding a sample size (n) of 71. We used a two-tailed t-test (two-sample assuming unequal variances) to determine whether the proportion of mussels consumed differed between fed and starved sea stars during winter (n=24).

We carried out a randomization (permutation) test (Sokal and Rohlf 2012) to test for a difference in the proportions of mussels consumed between winter and summer. We determined the probability of obtaining the observed difference between group means (D_0 = 21.7%) by calculating the proportion of values higher than D_0 (one-tail test) in a frequency distribution of 999 randomized differences. Each randomized difference was the difference between means for two groups of proportions (n = 24 and 71) drawn randomly from the 95 original proportions (24 in winter and 71 in summer) of mussels consumed. We preferred this statistical approach over a Student's t-test because it involves no assumption about the frequency distribution of the test statistic, and hence is a more robust approach to dealing with non-normal residuals and unequal sample sizes (Sokal and Rohlf 2012). All analyses were applied to the raw data.

Experiment 2: We used a two-way ANOVA with the factors Size (small or large sea stars) and Starvation (fed, starved for three weeks, and starved for six weeks), to examine

the effects of body size and starvation on the proportion of mussels consumed by *A. rubens* regardless of mussel size. Prior to running this two-way ANOVA, we used a two-way ANOVA with the factors Run (each of the three runs of four replicates of each treatment) and Block (each of the four blocks of one replicate of each treatment within a run) to determine if results differed among runs and blocks. There was no significant effect of Run ($F_{2,62}$=0.38, p=0.687) or Block ($F_{3,62}$=1.68, p=0.181), and hence we ran the two-way ANOVA on data pooled from all runs and blocks. Three large fed sea stars spawned during trials and we miscounted the initial number of mussels offered to one large 3-week starved sea star. These four data points were excluded from the analysis, yielding a sample size (n) of 68.

We used a two-way MANOVA with the factors Size (small or large sea stars) and Starvation (fed, starved for three weeks, and starved for six weeks), to examine the effects of body size and starvation on the proportion of mussels in each of three size classes (small, medium, and large) consumed by *A. rubens*. Prior to running this two-way MANOVA, we used a two-way MANOVA with the factor Run (each of the three runs of four replicates of each treatment) and Block (each of the four blocks of one replicate of each treatment within a run) to determine if results differed among runs and blocks. There was no significant effect of Run ($F_{2,62}$=0.65, p=0.691) or Block ($F_{3,62}$=0.65, p=0.753), and hence we ran the two-way MANOVA on data pooled from all runs and blocks. We excluded the same four data points as in the analysis described above, yielding a sample size (n) of 68. All analyses were applied to the raw data.

Experiment 3: We used a two-way ANOVA with the factors Crab (rock crabs alone, green crabs alone, or no crabs) and Mussel (presence or absence of crushed mussels) to

examine the effects of chemical cues on the proportion of mussels consumed by *A. rubens* regardless of mussel size. Prior to running this two-way ANOVA, we used a two-way ANOVA with the factors Run (each of the three runs of four replicates of each treatment) and Block (each of the four blocks of one replicate of each treatment within a run) to determine if results differed among runs and blocks. There was no significant effect of Run ($F_{2,62}$=0.81, p=0.449) or Block ($F_{3,62}$=0.61, p=0.609), and hence we ran the two-way ANOVA on data pooled from all runs and blocks. Rock crabs in three trials with crushed mussels, and rock crabs in one trial without crushed mussels, pushed the divider and entered the downstream section of the tank with *A. rubens*. These four data points were excluded from the analysis, yielding a sample size (n) of 68.

We used a two-way MANOVA with the factors Crab (rock crabs alone, green crabs alone, or no crabs) and Mussel (presence or absence of crushed mussels) to examine the effects of chemical cues on the proportion of mussels in each of the three size classes (small, medium, and large) consumed by *A. rubens*. Prior to running this two-way MANOVA, we used a two-way MANOVA with the factor Run (each of the three runs of four replicates of each treatment) and Block (each of the four blocks of one replicate of each treatment within a run) to determine if results differed among runs and blocks. There was no significant effect of Run ($F_{2,62}$=0.39, p=0.885) or Block ($F_{3,62}$=0.99, p=0.444), and hence we ran the two-way ANOVA on data pooled from all runs and blocks. We excluded the same four data points as in the analysis described above, yielding a sample size (n) of 68. All analyses were applied to the raw data.

In all ANOVAs and MANOVAs, homogeneity of the variance was verified by examining the distribution of the residuals. Normality of the residuals was verified by

examining the normal probability plot of the residuals (Snedecor and Cochran 1989). To detect differences among levels within a factor (ANOVAs and MANOVAs), we used Tukey HSD multiple comparison tests (comparisons based on least-square means) (Sokal and Rohlf 2012). When a factor or interaction between factors was significant in the MANOVAs, we examined the univariate model for the response variables to identify which one(s) contributed to the multivariate effect. This was done by conducting an ANOVA for the response variable with those factors that were significant in the MANOVA (Scheiner and Gurevitch 2001). The Pillai's trace multivariate statistic, which is more robust than other multivariate statistics to deviations from homoscedasticity and normality of the residuals, as well as more conservative with small and uneven sample sizes, was used in the MANOVA to determine which factor(s) were statistically significant (Scheiner and Gurevitch 2001). A significance level of 0.05 was used in all analyses, which were carried out with R 2.15.2. All means are presented with standard errors (mean ± SE) unless stated otherwise.

3.3. RESULTS

3.3.1. Experiment 1

Analysis of data from Experiment 1 indicated that the proportion of mussels consumed by small *Asterias rubens* during summer was not affected by temperature within the 8-to-15°C range, nor differed between fed and 3-week starved individuals (Table 3.1). The proportion of mussels consumed varied non-significantly from 28.0±6.5% in fed sea stars at 8°C to 49.1±6.4% in 3-week starved sea stars at 11°C

Table 3.1. Summary of two-way ANOVA (generalized linear model with binomial distribution, applied to raw data) examining the effect of Temperature (8, 11, and 15°C) and Starvation (fed and starved sea stars) on the proportion (out of 25) of mussels (*Mytilus edulis*) consumed by sea stars (*Asterias rubens*) during summer in Experiment 1 (see Section 3.2.2 for a description of the experiment).

Source of variation	*df*	χ^2	*p*
Temperature	2	4.23	0.120
Starvation	1	2.28	0.131
Temperature x Starvation	2	0.64	0.726

(Figure 3.2). Consumption during winter in water at 2°C also did not differ between fed (16.7±4.1%) and 3-week starved (22.7±4.5%) sea stars ($t_{0.05(2),22}$=-0.981, p=0.337; Figure 3.2). However, sea stars consumed twice more mussels in summer (41.4±2.5%) than winter (19.7±3.1%) (randomization test, p<0.001, Figure 3.2).

3.3.2. Experiment 2

Analysis of data from Experiment 2 indicated that the proportion of mussels consumed by *Asterias rubens* varied with body size among levels of starvation (a significant interaction between the factors Size and Starvation, Table 3.2). The proportion of mussels consumed ranged from 4.6±3.5% in large fed sea stars to 30.6±4.3% in large 3-week starved sea stars (Figure 3.3). Starvation had no perceptible effects on small sea stars as shown by the non-significant differences in mussels consumed by fed and starved individuals (Figure 3.3). However, it markedly affected large sea stars, with six times and twice more mussels consumed in 3-week starved individuals than in fed and 6-week starved individuals, respectively (Figure 3.3).

The MANOVA showed that body size and starvation affected the proportion of mussels consumed by *A. rubens* among the three mussel size classes (a significant interaction between the factors Size and Starvation, Table 3.3). However, effects of body size and starvation differed among mussel size classes (Table 3.4). Consumption of small (5-15 mm) mussels was influenced by body size only, being five times higher in small (13.2±2.0%) than large (2.5±0.1%) sea stars (Table 3.4, Figure 3.4). Consumption of medium (15-30 mm) mussels was affected by body size and starvation independently,

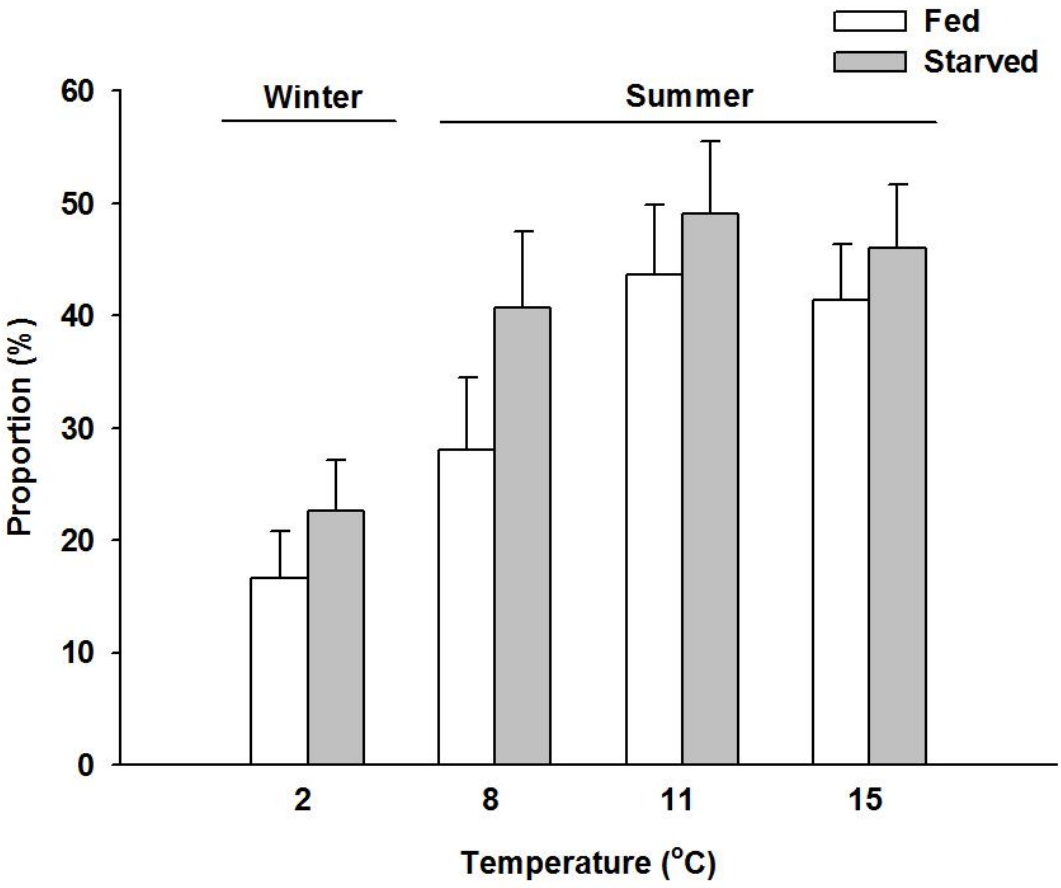

Figure 3.2. Mean (+SE) proportion (out of 25) of mussels (*Mytilus edulis*) consumed by small, fed or 3-week starved sea stars (*Asterias rubens*) in seawater at 2°C in winter, and at 8, 11, and 15°C in summer (Experiment 1). Temperature treatments not bracketed by the same horizontal line are different (data pooled across Temperature and Starvation treatments for the Winter versus Summer comparison; randomization test, $p<0.001$, n=24 and 71 for Winter and Summer, respectively).

Table 3.2. Summary of two-way ANOVA (applied to raw data) examining the effect of Size (small and large sea stars) and Starvation (fed, 3-week starved, and 6-week starved sea stars) on the proportion (out of 60) of mussels (*Mytilus edulis)* consumed by sea stars (*Asterias rubens*) in Experiment 2 (see Section 3.2.3 for a description of the experiment).

Source of variation	*df*	MS	F-value	*p*
Size	1	0.01	0.37	0.546
Starvation	2	0.13	9.09	<0.001
Size x Starvation	2	0.06	4.19	0.020
Error	62	0.01		
Corrected total	67			

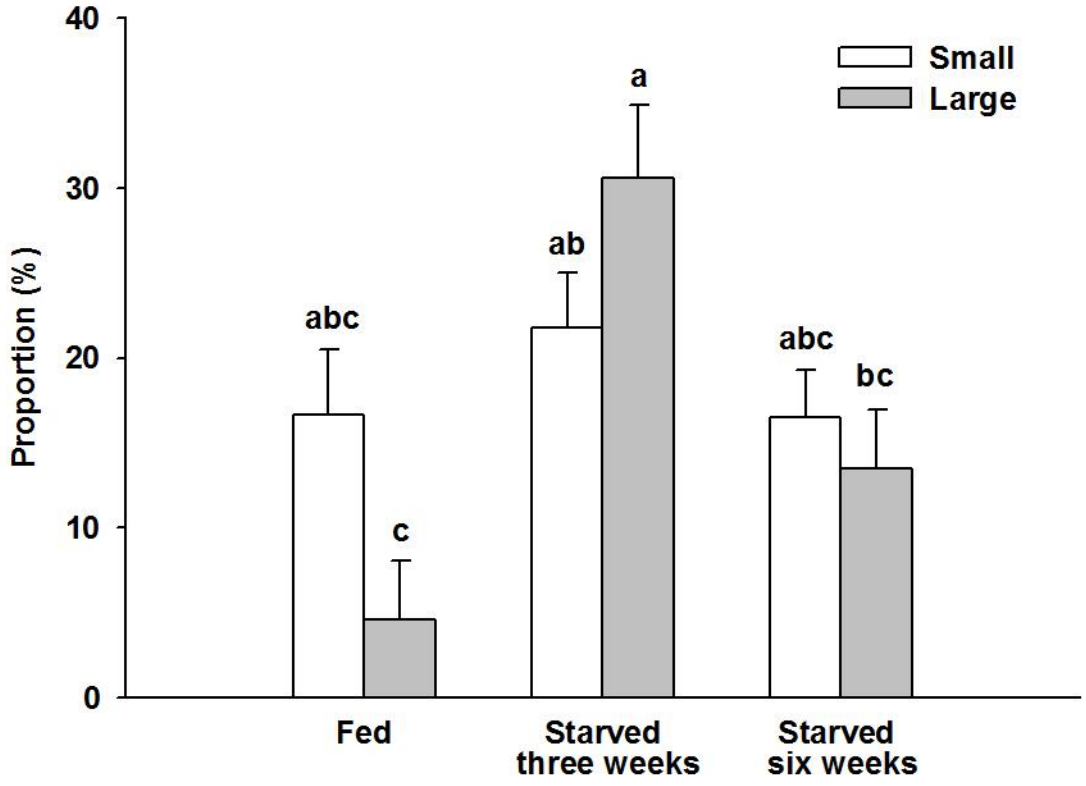

Figure 3.3. Mean (+SE) proportion (out of 60) of mussels (*Mytilus edulis*) consumed by small and large, fed or starved sea stars (*Asterias rubens*) (Experiment 2). Bars not sharing the same letter are different (LS means tests, $p<0.05$; n=12 for each combination of Size x Starvation, except 9 in large fed sea stars and 11 in large 3-week starved sea stars).

Table 3.3. Summary of two-way MANOVA (applied to raw data) examining the effect of Size (small and large sea stars) and Starvation (fed, 3-week starved, and 6-week starved sea stars) on the proportion (out of 20) of mussels (*Mytilus edulis*) in three size classes (small, medium, and large) consumed by sea stars (*Asterias rubens*) in Experiment 2 (see Section 3.2.3 for a description of the experiment).

Source of variation	Pillai	F-value	NumDF	DenDF	*p*
Size	0.052	21.69	3	60	<0.001
Starvation	0.277	3.28	6	122	0.005
Size x Starvation	0.270	3.17	6	122	0.006

Table 3.4. Summary of two-way ANOVAs (applied to raw data) examining the effect of Size (small and large sea stars) and Starvation (fed, 3-week starved, and 6-week starved sea stars) on the proportion (out of 20) of mussels (*Mytilus edulis*) in three size classes (small, medium, and large) consumed by sea stars (*Asterias rubens*) in Experiment 2 (see Section 3.2.3 for a description of the experiment).

Mussel size class	Source of variation	df	MS	F-value	p
Small (5-15 mm)	Size	1	0.194	22.61	<0.001
	Starvation	2	0.012	1.34	0.268
	Size x Starvation	2	<0.001	0.08	0.924
	Error	62	0.009		
	Corrected total	67			
Medium (15-30 mm)	Size	1	0.126	5.00	0.029
	Starvation	2	0.123	4.87	0.011
	Size x Starvation	2	0.034	1.33	0.272
	Error	62	0.025		
	Corrected total	67			
Large (30-45 mm)	Size	1	0.379	11.15	0.001
	Starvation	2	0.392	11.55	<0.001
	Size x Starvation	2	0.315	9.28	<0.001
	Error	62	0.034		
	Corrected total	67			

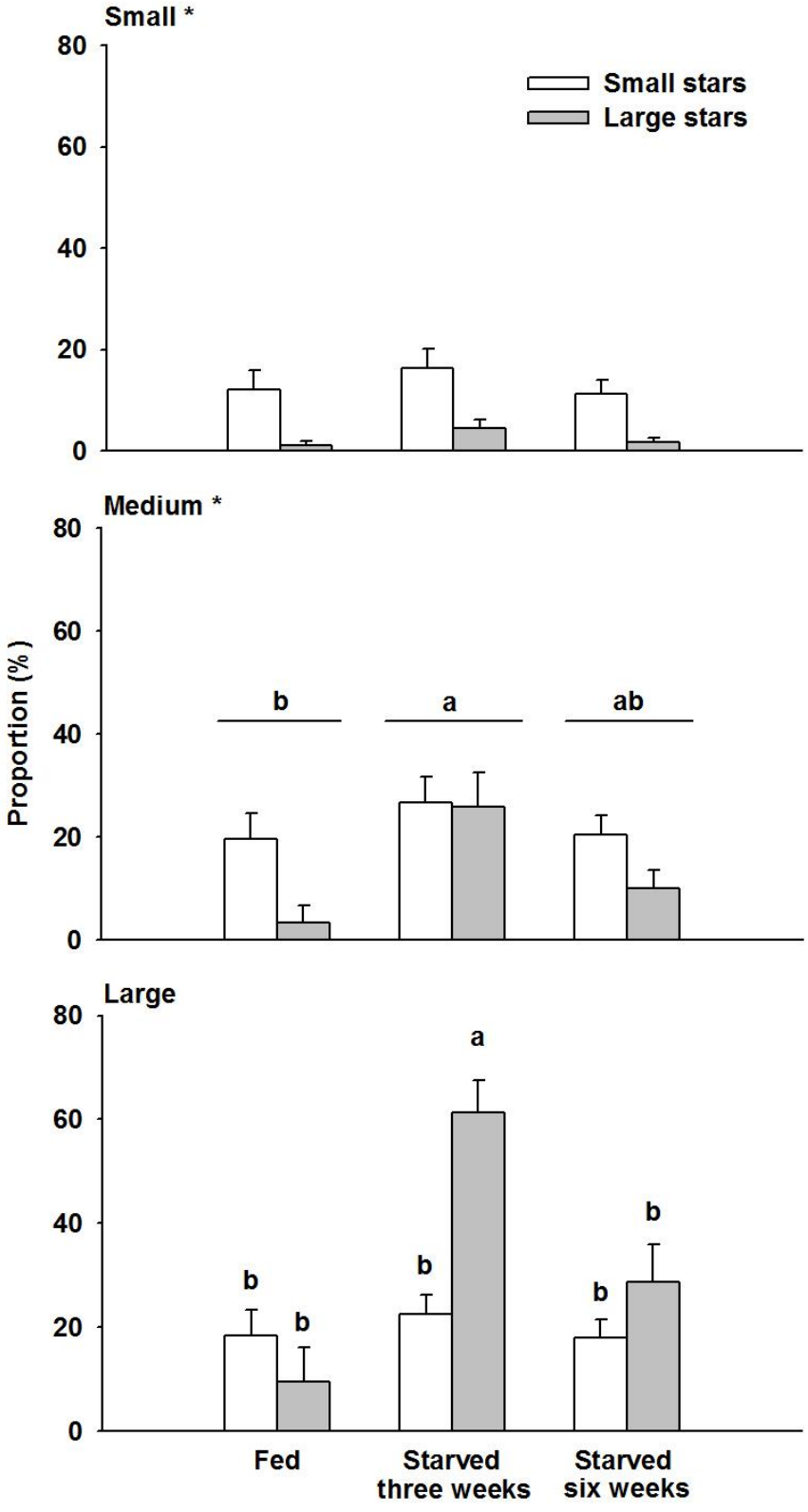
Small *
Small stars
Large stars
80
60
40
20
0
Medium *
Proportion (%)
b
a
ab
Large
a
b
b
b
b
b
Fed
Starved three weeks
Starved six weeks

Figure 3.4. Mean (+SE) proportion (out of 20) of mussels (*Mytilus edulis*) in three size classes (small, medium, and large) consumed by small and large, fed or starved sea stars (*Asterias rubens*) (Experiment 2). Panels with an asterisk indicate a significant difference in proportions between sea star sizes (Small>Large; data pooled across Starvation treatments). Bars not bracketed by the same horizontal line or not sharing the same letter (data pooled across sea star sizes for the medium mussel size class) are different (LS means tests, $p<0.05$; n=12 for each combination of sea star Size x Starvation, except 9 in large fed sea stars and 11 in large 3-week starved sea stars).

being ~1.5 times higher in small (22.2±2.7%) than large (13.6±3.2%) sea stars, and twice higher in 3-week starved (26.3±4.0%) than fed (12.6±3.6%) sea stars (Table 3.4, Figure 3.4). Consumption of large (30-45 mm) mussels, which peaked to 61.4±6.2% in large 3-week starved sea stars (Figure 3.4), varied with body size among levels of starvation (a significant interaction between the factors Size and Starvation, Table 3.4). It varied non-significantly with starvation in small sea stars and was at least twice higher in large 3-week starved sea stars than in large fed and 6-week starved individuals and small individuals of any starvation level (Figure 3.4).

3.3.3. Experiment 3

Analysis of data from Experiment 3 indicated that the proportion of mussels consumed by small, 3-week starved *Asterias rubens* was unaffected by chemical cues from potential competitors (the rock crab, *Cancer irroratus*, and the green crab, *Carcinus maenas*) and prey (the blue mussel, *Mytilus edulis*) (Table 3.5). The proportion of mussels consumed varied non-significantly from 14.9±3.1% in the presence of green crabs and crushed mussels to 22.9±4.1% in the presence of rock crabs alone (Figure 3.5).

The MANOVA also showed no detectable effects of chemical cues on the proportion of mussels in each of three size classes consumed by *A. rubens* (Table 3.6). Consumption of small (5-15 mm) mussels varied non-significantly from 13.7±3.8% in the presence of crushed mussels alone to 32.2±7.9% in the control treatment without crabs and crushed mussels (Table 3.6, Figure 3.6). Consumption of medium (15-30 mm) mussels varied non-significantly from 28.7±5.9% in the presence of crushed mussels

Table 3.5. Summary of two-way ANOVA (applied to raw data) examining the effect of Crab (rock crabs alone, green crabs alone, or no crabs) and Mussel (presence or absence of crushed mussels) on the proportion (out of 60) of mussels (*Mytilus edulis*) consumed by sea stars (*Asterias rubens*) in Experiment 3 (see Section 3.2.4 for a description of the experiment).

Source of variation	*df*	MS	F-value	*p*
Crab	2	0.013	1.05	0.358
Mussel	1	0.004	0.29	0.594
Crab x Mussel	2	0.021	1.71	0.190
Error	62	0.013		
Corrected total	68			

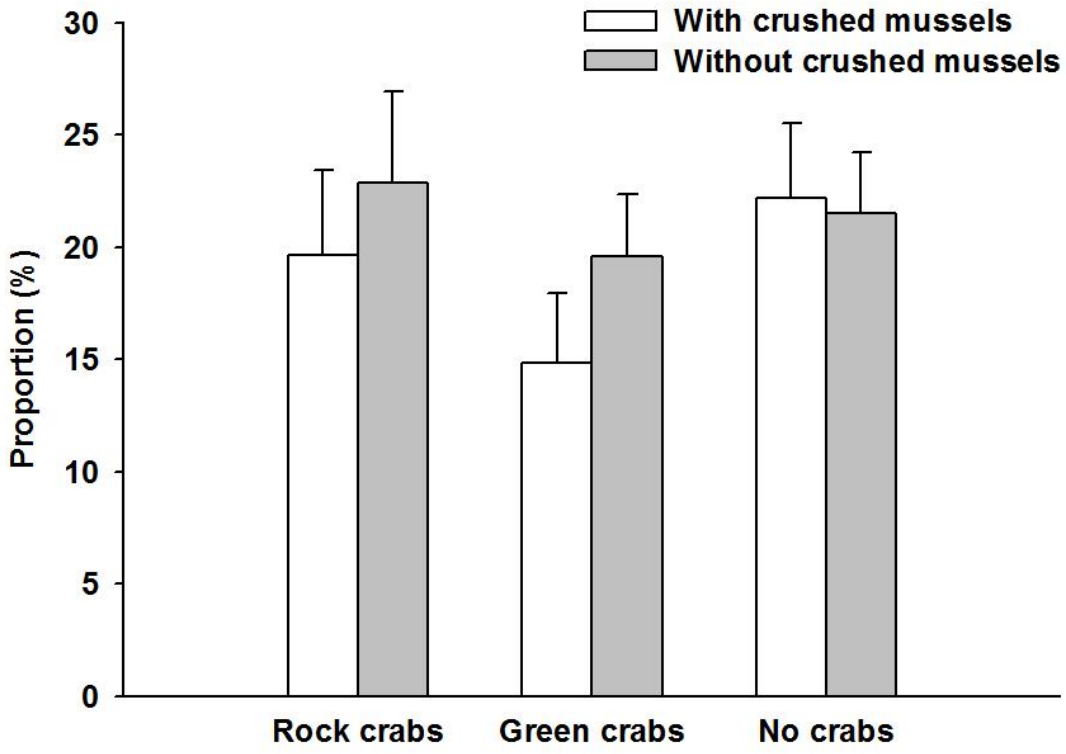

Figure 3.5. Mean (+SE) proportion (out of 60) of mussels (*Mytilus edulis*) consumed by small, 3-week starved sea stars (*Asterias rubens*) in the presence or absence of chemical cues from rock crabs (*Cancer irroratus*), green crabs (*Carcinus maenas*), and crushed *M. edulis* (Experiment 3) (n=12 for each combination of Crab x Mussel, except 9 in rock crabs with crushed mussels and 11 in rock crabs without crushed mussels).

Table 3.6. Summary of two-way MANOVA (applied to raw data) examining the effect of Crab (rock crabs alone, green crabs alone, or no crabs) and Mussel (presence or absence of crushed mussels) on the proportion (out of 20) of mussels (*Mytilus edulis)* in three size classes (small, medium, and large) consumed by sea stars (*Asterias rubens*) in Experiment 3 (see Section 3.2.4 for a description of the experiment).

Source of variation	Pillai	F-value	NumDF	DenDF	*p*
Crab	0.102	1.08	6	122	0.374
Mussel	0.011	0.21	3	60	0.887
Crab x Mussel	0.084	0.89	6	122	0.502

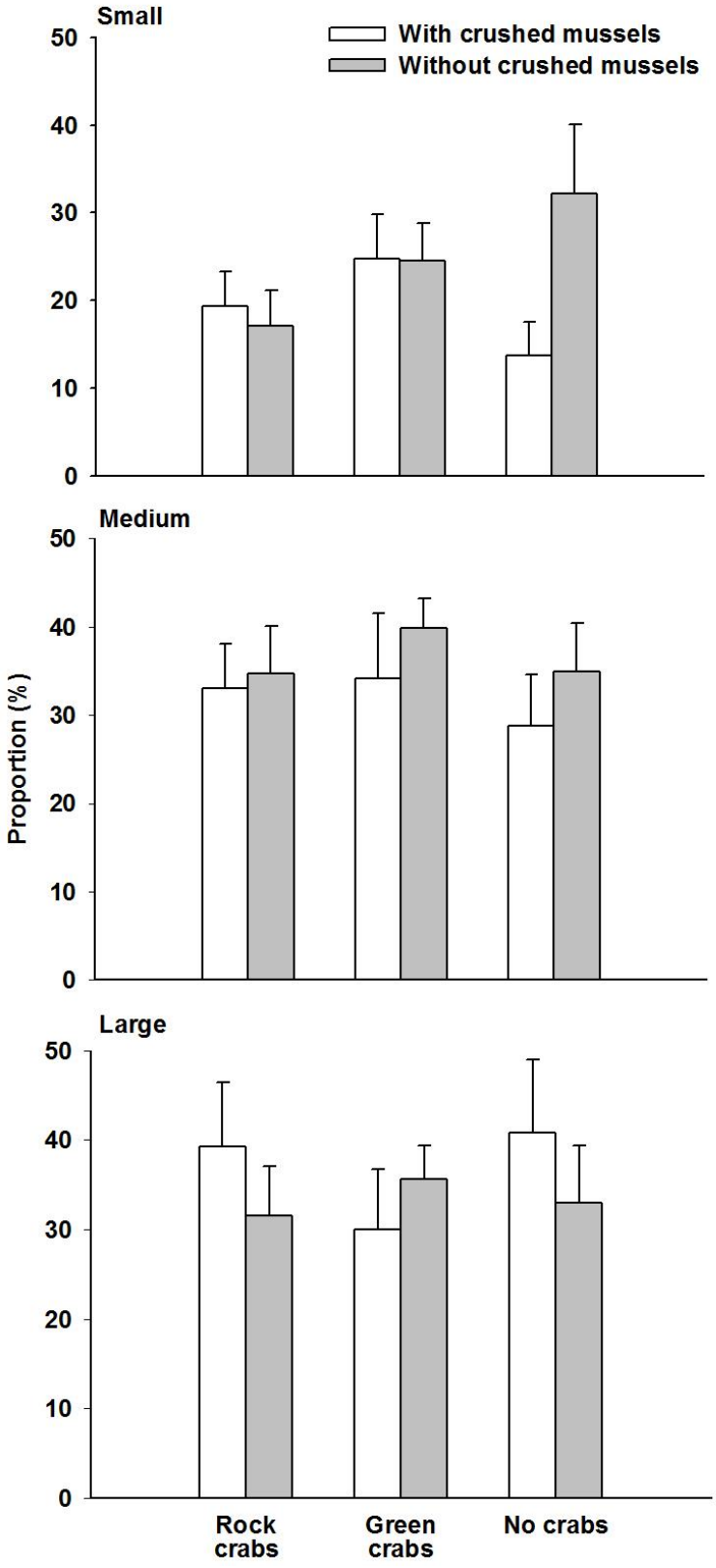
Small
With crushed mussels
Without crushed mussels
50
40
30
20
10
0
Medium
Proportion (%)
Large
Rock crabs
Green crabs
No crabs

Figure 3.6. Mean (+SE) proportion (out of 20) of mussels (*Mytilus edulis*) in three size classes (small, medium, and large) consumed by small, 3-week starved sea stars (*Asterias rubens*) in the presence or absence of chemical cues from rock crabs (*Cancer irroratus*), green crabs (*Carcinus maenas*), and crushed *M. edulis* (Experiment 3) (n=12 for each combination of Crab x Mussel, except 9 in rock crabs with crushed mussels and 11 in rock crabs without crushed mussels).

alone to 39.9±3.3% in the presence of green crabs alone (Table 3.6, Figure 3.6). Consumption of large (30-45 mm) mussels varied non-significantly from 30.0±6.7% in the presence of green crabs and crushed mussels to 40.9±8.1% in the presence of crushed mussels alone (Table 3.6, Figure 3.6).

3.4. DISCUSSION

Our study demonstrates that mussel (*Mytilus edulis*) consumption and size selection in *Asterias rubens* from southeastern Newfoundland is strongly affected by the sea star's body size and degree of starvation, and to a lesser extent by water temperature in late summer. A first indication that feeding in *A. rubens* is relatively insensitive to water temperature in late summer is provided by our finding in Experiment 1 that small (9-15 cm), fed and 3-week starved sea stars consumed similar proportions (at least 28%) of medium-sized (15-30 mm) mussels at 8, 11, and 15°C. In contrast, Barbeau and Scheibling (1994b) found that small (8-10 cm) *A. rubens* from Nova Scotia consumed nearly four times more Atlantic deep-sea scallops (*Placopecten magellanicus*) at 15 than 8°C during summer. The authors attributed this difference to increased searching movement velocities in *A. rubens* and reduced scallop handling time and effectiveness of escape response at 15°C (Barbeau and Scheibling 1994b). Differences in behavioral and morphological traits of prey may help explain this inconsistent outcome between both studies. But, as explained below, we also think that it largely stems from different thermal acclimations of sea stars prior to experimentation.

Sea stars in Experiment 1 were not pre-acclimated to their respective experimental temperature treatments. This procedure was used to more accurately account for effects of short-term, natural variability in sea temperature in coastal Newfoundland (Caines and Gagnon 2012; Blain and Gagnon 2013) on sea star feeding. Accordingly, our results reflect the ability of small *A. rubens* to adapt feeding to relatively sharp temperature changes (in this study up to 5.4°C) during a specific period (September). In their study, Barbeau and Scheibling (1994b) pre-acclimated *A. rubens* for five to seven days to their respective experimental temperature treatments. Sea stars in the latter study therefore had much more time to physiologically and behaviorally adapt to specific steady temperature regimes, which are uncommon in summer in eastern Canadian rocky subtidal habitats inhabited by *A. rubens* (Lauzon-Guay and Scheibling 2007; Scheibling and Gagnon 2009; Caines and Gagnon 2012; Blain and Gagnon 2013; Gagnon et al. 2013). These longer adaptation times could well explain why temperature affected the sea star's feeding response in Barbeau and Scheibling (1994b) but not in the present study.

Our finding that *A. rubens* consumed 52% less mussels in the winter than summer runs of Experiment 1, when mean sea temperature was respectively ~2 and ~13°C, strongly suggests that feeding is sensitive to long-term (seasonal) effects of sea temperature changes. This seasonal increase in feeding is consistent with the observations of Gaymer et al. (2002) for *A. rubens* in the northern Gulf of St. Lawrence. Mussel meat weight and protein and glycogen contents are generally lowest in late winter (Zandee et al. 1980; Okumuş and Stirling 1998). Sea stars in our experiment would have had to consume a greater number of mussels in winter than summer to obtain the same amount

of energy, which was not the case. It therefore seems that the observed seasonal differences in feeding were mainly caused by a lower metabolism in winter in *A. rubens*, and to a much lesser extent by likely lower mussel profitability in winter. Although in our experiment temperature was confounded by time (season), it is arguably a better representation of likely seasonal variation of the sea star's feeding. Other environmental factors such as day length, salinity, and the concentration of oxygen in the water column change with season (Pinet 2011) and may also affect the sea star. Yet, temperature is the primary factor that influences metabolism and behavior in ectothermic organisms like *A. rubens* (Gillooly et al. 2001; Brown et al. 2004b; Harley 2013). Studies of *A. rubens* in European seas also found reduced feeding in winter compared to summer (Hancock 1958; Anger et al. 1977; Aguera et al. 2012). This pattern could be caused by higher metabolic demand in summer together with accumulation of glycogen in the pyloric caeca, which both require higher food consumption (Jangoux and van Impe 1977). In a concurrent study, Frey and Gagnon (Frey and Gagnon (In press)) showed that kelp consumption in early summer (June-July) by green sea urchins (*Strongylocentrotus droebachiensis*) from southeastern Newfoundland obeyed a non-linear, size- and temperature-dependent relationship. Feeding in large urchins was consistently highest and positively correlated with temperature <12°C and dropped within and above the 12-15°C tipping range (Frey and Gagnon (In press)). As in Experiment 1, urchins in the latter study were not pre-acclimated to their experimental temperature treatments, which ranged from 3 to 18°C. Yet, the authors modeled mean daily rates of kelp bed destruction by urchin fronts over nearly three months with an accuracy of 88% based uniquely on the temperature-

dependent relationship derived from a laboratory experiment similar to Experiment 1, sea temperature, and urchin abundance at one subtidal site (Frey and Gagnon (In press)). Collectively, these findings speak to the importance of considering natural variation in sea temperature at multiple temporal scales if we are to accurately predict causes and consequences of alterations to predator-prey interactions.

Results of Experiment 2 corroborated the conclusion from Experiment 1 that moderate (3-week) starvation has no perceptible effect on mussel consumption in small *A. rubens*. But we also found with Experiment 2 that consumption of small, severely (6-week) starved sea stars was similar to that of small, fed and moderately starved sea stars. In contrast, consumption of large (25-30 cm), moderately starved *A. rubens* was respectively six times and twice higher than that of large, fed and severely starved individuals. These findings have several important conceptual implications. Firstly, they indicate that the need to feed after a relatively short period (~3 weeks) of food deprivation is considerably higher in large than small *A. rubens*. Sea stars, including *A. rubens* in eastern Canada, often form dense feeding aggregations in mussel beds (Sloan and Aldridge 1981; Dare 1982; Gaymer and Himmelman 2002; Scheibling and Lauzon-Guay 2007). Once sea star aggregations eliminate mussels and other prey from an area, they move away in search of other prey patches (Sloan 1980; Menge 1982; Robles et al. 1995; Gaymer et al. 2001a). By being less sensitive than large conspecifics to effects of moderate starvation, small *A. rubens* should be better adapted to low food conditions, and hence more likely to quickly resume normal feeding upon reaching the next available prey patch. Secondly, they indicate that large *A. rubens* attempt to compensate for the

lack of food-derived energy: 1) mainly behaviorally by increasing prey consumption when starvation does not exceed ~3 weeks, and 2) perhaps physiologically by more intensively catabolizing reserve material from specialized organs when starvation exceeds ~3 weeks. The latter suggestion is based on several studies that showed that the release of reserve material from pyloric caeca in *A. rubens* and other sea stars suffice to ensure survival for two to four weeks of starvation, after which general autolysis occurs (Chia 1969; Jangoux and van Impe 1977; Xu and Barker 1990). If large *A. rubens* in Experiment 2 had pyloric reserves that they could use for up to six weeks, then mussel consumption after six weeks of starvation would have been at least as high as after three weeks of starvation. Yet, consumption was half lower in 6- than 3-week starved sea stars, suggesting that general autolysis after six weeks of starvation had begun. Interestingly, our data also suggest that small *A. rubens* did not deplete pyloric reserves for up to at least six weeks of starvation for mussel consumption was similar among small, fed and 3- and 6-week starved individuals.

The universal quarter-power allometric relationship by which biological rate processes in most animals scale with body size (Gillooly et al. 2001) helps explain why the suggested depletion of pyloric reserves occurred in large but not small *A. rubens*. Indeed, the mass-specific metabolic rate of an organism, B/M, scales with body mass, M, such that $B/M \propto M^{-1/4}$ (Gillooly et al. 2001). Accordingly, large sea stars must, in theory, sustain a constantly higher metabolic rate than smaller individuals, and hence deplete their pyloric reserves more quickly. However, Raymond et al. (2007) showed that energetic content (lipids and carbohydrates) of pyloric caeca in *A. rubens* decreased

during one spawning season in the northern Gulf of St. Lawrence. We did not measure pyloric caeca in the present study, and hence cannot rule out the possibility that pyloric reserves may have been affected by reproduction. We minimized this potential effect by discarding the only sea star that spawned prior to trials, as well as trials during which sea stars spawned (three out of 72).

Experiment 2 also showed that the consumption of small (5-15 mm), medium (15-30 mm), and large (30-45 mm) mussels by *A. rubens* was respectively affected by the sea star's size only, size and starvation independently, and size and starvation interactively. This finding indicates that an increasingly complex set of morphological and physiological parameters governs the decision or ability of *A. rubens* to consume mussels as both organisms get larger. Size therefore matters, which aligns with the empirical demonstration that feeding rates in *A. rubens* from the Baltic Sea increase slightly more than cubically with the size of the sea star, and slightly more than linearly with the body mass of the sea star (Sommer et al. 1999). Hummel et al. (2011) examined consumption of *M. edulis* in five size classes (from 3 to 55 mm) by *A. rubens* from the Wadden Sea and concluded that the sea star generally selects mussels that are smaller than those with the highest profitability (ratio of prey energy content to the time required for handling the prey, Emlen 1966; MacArthur and Pianka 1966). A similar inclination to feed upon energetically sub-optimal prey sizes has been shown in other types of predators, including green crab (*Carcinus maenas*, Johnstone and Norris 2000), Dungeness crab (*Metacarcinus magister*, formerly *Cancer magister*, Juanes and Hartwick 1990), and oystercatcher (*Haematopus ostralegus*, Smallegange and Van der Meer 2003). It is generally viewed as a mechanism to avoid damaging predatory organs (e.g. eversible

stomachs of sea stars, chelae of crabs, bills of shorebirds) when attempting to penetrate or crush larger and harder shelled prey (Juanes and Hartwick 1990; Johnstone and Norris 2000; Smallegange and Van der Meer 2003; Hummel et al. 2011). Our finding in Experiment 2 that small sea stars consumed significantly higher proportions of small and medium mussels than large sea stars, which in turn consumed significantly more large mussels than small sea stars, supports the notion that *A. rubens* selects mussels based on profitability. Large, moderately starved sea stars increased their consumption of large mussels by more than six times compared to large, fed sea stars. This result strongly suggests that large mussels are the most profitable to *A. rubens* and that starvation can alter the normal pattern of consumption of large mussels by large sea stars.

Chemical cues regulate critical aspects of the behavior of most marine organisms, while determining foraging strategies and competitive interactions in many benthic invertebrate consumers (Hay 2009). Sea stars, including *A. rubens*, primarily use chemodetection to locate prey and competitors (Castilla and Crisp 1970; Zafiriou et al. 1972; Gaymer et al. 2002; Drolet and Himmelman 2004). We showed with Experiment 3 that chemical cues from two potential competitors in southeastern Newfoundland, the indigenous rock crab (*Cancer irroratus*) and invasive green crab (*Carcinus maenas*), had no effect on mussel consumption and size selection in small, 3-week starved *A. rubens*. The presence of crushed mussels in the vicinity of *A. rubens* also did not elicit a change in feeding whether crabs were present or absent. We propose that *A. rubens* maintained mussel consumption regardless of crab chemical cues for they did not perceive these cues as a threat or perceived them as a threat that only requires greater vigilance, as seen in other benthic consumers (Hazlett and McLay 2000; Brown et al. 2004a; Matheson and

Gagnon 2012b). Sea stars used in the present study were collected along the south shore of Conception Bay where rock crab is present but green crab has not been reported yet (DFO 2010, P. Gagnon, personal observations). It is therefore likely that green crab chemical cues were new to the sea stars, and hence that the latter did not respond to those cues. That mussel consumption in Experiment 3 was similar to that of small, 3-week starved sea stars in Experiment 2 in which there was no crab, further supports the notion that *A. rubens* does not perceive chemical cues from these crabs as a threat (or at all) or that these species do not compete. Further studies are required to determine if the sea star would change consumption upon physical contact with crabs.

In summary, our experimental approach to the study of mussel prey consumption and size selection in *A. rubens* from southeastern Newfoundland provides the first compelling evidence that starvation, body size, and their interaction are key determinants of its feeding ecology. Consumption is relatively stable across the natural temperature range in late summer, significantly lower in winter than summer when mean sea temperature is respectively ~2 and ~13°C, and unaffected by the chemical presence of rock and green crabs. These findings add to a companion study in which we showed that wave action and starvation modulate displacement, microhabitat selection, and ability to contact mussel prey in small *A. rubens* from southeastern Newfoundland (Chapter II). Long-term experimental and mensurative field studies are required to test the generality of our results and to better understand how body size and starvation interact with the thermal and hydrodynamic environment in shaping natural *A. rubens* and *M. edulis* populations in Newfoundland. Collectively, our findings speak to the importance of

considering the interplay between organismal traits and ongoing changes in ocean climate (Halpern et al. 2008; Burrows et al. 2011) to more accurately predict causes and consequences of alterations to northern reef communities.

CHAPTER IV

Summary

4.1. Overall objective of the study

The common sea star, *Asterias rubens,* is a major predator in rocky subtidal ecosystems in the northern Gulf of St. Lawrence and along the Atlantic coast of Newfoundland, Canada. In these highly seasonal systems, *A. rubens* primarily consumes bivalve prey, with a strong preference for the blue mussel, *Mytilus edulis*. Knowledge about foraging of *A. rubens* in eastern Canada is largely based on a few laboratory and field studies in the northern Gulf of St. Lawrence, which examined prey preference, mussel (*M. edulis*) consumption and size selection, interspecific competition for prey, and displacement under various hydrodynamic conditions. Collectively, these studies established that *A. rubens* is a highly selective predator, even when prey abundance is limiting. But they also suggested that foraging in *A. rubens* is governed by a complex suite of biotic and abiotic factors.

The overall objective of this research was to test effects of key biotic (body size, starvation, chemical cues from potential competitors) and abiotic (temperature, wave action) factors on: 1) displacement, microhabitat selection, and ability to contact mussel [*M. edulis*] prey [Chapter II]; and 2) mussel prey consumption and size selection [Chapter III] in *A. rubens* to gain a better understanding of the mechanistic underpinnings of foraging variability for the species. Work involved experiments in laboratory microcosms (wave tank and aquaria) at the Ocean Science Center of Memorial University of Newfoundland with *A. rubens* from various subtidal sites along the south shore of Conception Bay, as well as analysis of seabed imagery and temperature and wave data from Bread and Cheese Cove (BCC) in Bay Bulls, southeastern Newfoundland.

4.2. Displacement, microhabitat selection, and ability to contact prey

Chapter II tested the hypothesis that wave action and starvation modulate displacement, microhabitat selection, and ability of *A. rubens* to contact mussel (*M. edulis*) prey. Specifically, we used an oscillatory wave tank that mimics the back-and-forth flow caused by waves in shallow subtidal habitats to quantify, at three wave velocities [0.0 m s^{-1} (Null), 0.1 m s^{-1} (Low), and 0.2 m s^{-1} (High)]: 1) linear displacement, dislodgement, and time spent in six microhabitats mimicking natural seabed heterogeneity [Experiment 1]; and 2) ability to contact mussels [Experiment 2], in small [9-15 cm], fed and 3-week starved sea stars. We carried out both experiments in two seasons when sea temperature differed markedly (~2°C and 13°C) to quantify intra-annual variation in the effects of wave action and starvation. We also 3) studied relationships between changes over six months in the abundance of *A. rubens* and the wave and temperature environment at three depths [2, 4, and 8 m] at BCC.

Experiment 1 showed that *A. rubens* displaced up to 50% less with increasing wave velocity. Displacement was 120% higher in summer than winter, and lower in starved than fed individuals in summer only. The sea star predominantly stayed on flat horizontal surfaces, did so more frequently in the presence than absence of waves, and spent more time in the two most uneven microhabitats in winter than summer regardless of wave velocity. Experiment 2 showed that more sea stars left the centre of a depression surrounded by mounds and reached the top of the mounds in summer than winter, in the absence than presence of waves, and when starved than fed. Sea stars that reached the top of mounds spent more time there in the presence than absence of mussels in summer only,

when starved than fed in summer only, and in the presence than absence of mussels at null and low wave velocities. Measurements of wave height, sea temperature, and *A. rubens* abundance over six months at BCC indicated that the sea star was >4 times more abundant at 8 m than at 2 m and 4 m. This difference was unrelated to temperature and likely caused by the wave environment.

4.3. Prey consumption and size selection

Chapter III tested the effects of water temperature, starvation, body size, and chemical cues from potential crustacean competitors on mussel (*M. edulis*) consumption and size selection in *A. rubens*. Specifically, we quantified 1) consumption of medium [15-30 mm] mussels by small [9-15 cm] sea stars fed or starved moderately [for three weeks] at three temperatures representative of middle-to-late summer highs [8, 11, and 15°C] and one temperature typifying late winter lows [2°C] [Experiment 1]; 2) consumption of small [5-15 mm], medium, and large [30-45 mm] mussels by small and large [25-30 cm] sea stars fed or starved moderately or severely [for six weeks] [Experiment 2]; and 3) consumption of small, medium, and large mussels by small sea stars starved moderately, in the presence or absence of chemical cues from *C. irroratus*, *C. maenas*, and crushed mussels [as an incentive to feed] [Experiment 3].

Experiment 1 showed that temperature and starvation did not affect consumption in summer, which was twice higher than in winter. Starvation also did not affect consumption in winter. Experiment 2 showed that small sea stars consumed similar proportions of mussels regardless of starvation. However, large moderately starved sea

stars consumed respectively six times and two times more mussels than large, fed and severely starved sea stars, indicating that the need to feed after a relatively short period of food deprivation was considerably higher in large than small *A. rubens*. Consumption of small, medium, and large mussels was respectively affected by the sea star's size only, size and starvation independently, and size and starvation interactively. Experiment 3 showed that neither crabs, nor crushed mussels affected mussel consumption and size selection.

4.4. Importance of the study

The present study provides the first quantitative analysis of the effects of some of the main drivers of changes in displacement, microhabitat selection, ability to contact prey, prey consumption, and prey size selection in *Asterias rubens* from Newfoundland. Chapter II demonstrated that wave action, and to a lesser extent starvation, are key modulators of the sea star's inclination and ability to explore its environment and localize prey. In southeastern Newfoundland, the behavioral response of *A. rubens* to wave action and starvation is adaptable, being generally stronger in summer than winter, when sea temperature differs markedly. Chapter III established that starvation, body size, and their interaction are key determinants of the feeding ecology of *A. rubens*. Consumption is relatively stable across the natural temperature range in late summer, significantly lower in winter than summer when mean sea temperature is respectively ~2 and ~13°C, and unaffected by the chemical presence of rock and green crabs. The present study therefore significantly increases knowledge about the mechanistic underpinnings of foraging

variability in *A. rubens* in eastern Canada. It also speaks to the importance of considering the interplay between organismal traits and ongoing changes in ocean climate to more accurately predict causes and consequences of alterations to northern reef communities.

4.5. Future directions

The present study provides a framework for further research on the environmental and physiological factors that influence displacement, microhabitat use, and feeding in *Asterias rubens* from Newfoundland. Further studies should attempt to resolve the full spectrum of biotic (e.g. presence of potential predators, reproductive stage) and abiotic (e.g. salinity, light conditions) factors that affect the limits of tolerance, behavioral adaptability, and feeding plasticity of *A. rubens* to environmental variability. Except for one field component in Chapter II, results presented in this thesis are entirely based on laboratory microcosm experiments under controlled conditions. These experiments were a necessary first step to separate the individual effects of each factor and measure the strength of their interactions. Long-term experimental and mensurative field studies are required to better understand how body size and starvation interact with thermal and hydrodynamic environments in natural settings. In the absence of such knowledge, the capacity to predict and mitigate consequences of alterations to *A. rubens* populations at the community level under a changing ocean climate will remain limited.

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APPENDIX A

Complementary trials for Experiment 1 (Chapter II)

We carried out complementary trials under a paired comparison design to determine if the distance moved by any one sea star in Experiment 1 could be affected by the presence of the other sea star. As discussed by Montgomery (2008), in a paired comparison design two experimental treatments are successively applied once, in a random order, to each individual from a pool of individuals. The difference in the response variable between treatments is calculated for each individual, yielding multiple differences that can be null, positive, or negative. A one-sample t-test can then be used to determine if the mean difference from all individuals is statistically different from zero (0), in which case one would conclude that treatments effects differ. Accordingly, we used the same experimental setup and procedures as in Experiment 1 to compare the distances moved over 30 minutes, both alone and in the presence of one conspecific, of each of 24 sea stars at null and 24 sea stars at low, wave velocity. The mean difference in distance moved between sea stars with and without a conspecific was 7.3±6.1 [SE] cm and -1.1±5.7 cm at null and low wave velocity, respectively. Both differences were not significantly different than zero (null velocity: $t_{\alpha=0.05,23}$=1.19, p=0.245; low velocity: $t_{\alpha=0.05,23}$=-0.18, p=0.853). We therefore concluded that the distance moved by one sea star was not affected by the presence of the other sea star.

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